The Canadian Entomologist

Vol. LXXXVII Ottawa, Canada, October 1955 No. 10

Studies on the Starvation of Last-Instar Larvae of the Larch Sawfly, *Pristiphora erichsonii* (Htg.) (Hymenoptera: Tenthredinidae)[1]

By R. J. Heron[2]
Forest Biology Laboratory
Winnipeg, Man.

INTRODUCTION

Larvae of the larch sawfly, *Pristiphora erichsonii* (Htg.), feed on the foliage of conifers of the genus *Larix*. In Manitoba and Saskatchewan, where the studies described here were conducted, the native host is tamarack, *L. laricina* (Du Roi) K. Koch. At outbreak population levels larval feeding commonly causes complete defoliation. Trees show a marked reduction in foliage production after three or four successive years of severe defoliation (6). As a consequence, larval starvation is commonly associated with declining host vigour. Starvation reduces the population size directly by causing larval mortality and indirectly by reducing the reproductive capacity of the partially starved survivors. This paper deals primarily with the measurement of the sub-lethal effects of starvation during the last larval stadium as studied in laboratory-reared and field-collected insects.

EXPERIMENTALLY INDUCED STARVATION

Last-instar larvae were subjected to varying degrees of food deprivation, in the laboratory, to determine their susceptibility to starvation. For this experiment, larvae in their penultimate (fourth) stadium were collected in a tamarack stand in the southern portion of the Whiteshell Forest Reserve near Telford, Manitoba. Following the fourth molt, the larvae were divided into six groups each of which was allowed to feed for a specified period as indicated in Table I.

Larvae which were starved for an initial period prior to feeding, (including those which were completely deprived of food), were kept in closed glass jars containing moist absorbent cotton. This prevented weight loss and death due to

[1]Contribution No. 231, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.
[2]Research Officer.

Table I

Mortality and Development of Fifth-instar Larvae Subjected to Varying Degrees of Starvation

Group	Treatment	Initial number of larvae	Per cent mortality	Mean no. of days in fifth stadium prior to cocooning
I	Fed throughout stadium (Controls)	50.	0.0	9.4
II	Starved for 3 days and then fed	50.	0.0	11.8
III	Fed for 5 days and then starved	41.	63.4	8.0
IV	Fed for 3 days and then starved	47.	93.6	13.3
V	Starved for 5 days and then provided with food	50.	100.0	–
VI	Starved throughout the fifth stadium	50.	100.0	–

desiccation. After removal from food or cessation of feeding the larvae were placed in covered tins containing damp sphagnum moss to provide suitable conditions for cocooning. Larvae that successfully formed cocoons were removed from the tins and packed in moist moss. Early in September they were stored at 1-3°C.

Effects of Starvation on Pre-cocooning Mortality

Data pertaining to the mortality of larvae in the experimental rearings are presented in Table I. The mean duration of the feeding period of the fifth-instar larvae of the control group was 9.4 days. Larvae which fed for three days during the fifth stadium were found to consume slightly less than half as much foliage as fully-fed larvae. Twenty per cent of the total larval feeding takes place during the first four stadia (4) and an additional 20 to 30 per cent of the consumption occurs during the first three days of the fifth stadium. These larvae suffered almost 100 per cent mortality indicating that food consumption must be in excess of 50 per cent of the normal requirement to permit the larvae to complete their development successfully.

Larvae which were deprived of foliage throughout the fifth stadium exhibited considerable motor activity during the initial part of the starvation period. Under natural conditions this accelerated activity undoubtedly would have survival value for the larvae in their search for food. The intensity of this activity was not measured but it was observed that it declined sharply after two or three days starvation. After four or five days, the larvae, although still alive, were completely immobilized and could not feed, even when foliage was made available.

Sub-lethal Effects of Starvation

The Duration of the Pre-cocooning Period

The duration of the pre-cocooning period, i.e. the time from the beginning of the fifth stadium until the commencement of cocoon formation, was markedly influenced by partial starvation. The mean duration of the pre-cocooning period for each of the experimental groups is given in Table I. In the case of the few larvae which survived after having fed only three days, cocoon formation was postponed for about four days. In contrast, the larvae which fed for an initial period of five days, and were then deprived of food, cocooned about one day earlier than the controls. Those larvae which were deprived of food for an initial period of three days and were then allowed to feed, continued to feed for a period only slightly less than the control group. The initial starvation period in this group delayed the inception of cocooning without appreciably affecting the duration of the feeding period.

The Weights and Lipid Content of Diapausing Larvae

The weights and lipid content of diapausing larvae from the various rearings were compared. In late December and early January the diapausing larvae (eonymphs (7)) were removed from cold storage, taken from their cocoons, and weighed. They were then dried in vacuo at 50°C., stored over anhydrous calcium chloride and their dry weights determined. The dried larvae were extracted for twenty-four hours in a Soxhlet extractor using a solvent-mixture of 2.5 parts anhydrous ethyl ether and 1 part absolute ethyl alcohol (1). Lipic content was calculated as the difference in weight before and after extraction.

The fifth stadium is a period of rapid weight increase and accumulation of reserves, particularly of fats. Premature termination of feeding arrests this storage activity. Subsequent energy expending processes, particularly pre-diapause activities such as cocoon formation, reduce the accumulated reserves.

TABLE II

The Weights, Lipid and Water Contents of Eonymphs of Fully-fed and Partially-starved Larvae

Group	Mean duration of feeding period (days)	No. of eonymphs weighed	Wet weight (mg.)		Dry weight (mg.)		Lipid content (mg.)		Per cent water content	Lipid content as per cent of wet weight	Lipid content as per cent of dry weight
			Mean	S.E. ±	Mean	S.E. ±	Mean	S.E. ±			
I	9.4	9	44.9	1.5	18.4	0.4	7.7	0.7	63.4	17.0	41.6
II	8.8	8	44.1	2.5	16.1	0.8	6.9	0.6	68.9	15.6	40.5
III	5.0	19	39.7	1.1	14.9	0.4	5.4	1.1	66.8	13.4	35.8
IV	3.0	4	33.7	2.1	9.1	0.5	2.9	0.4	73.2	8.4	31.5
F	–	–	5.9*		21.4*		9.1*		1.6	8.8*	2.0

*Significantly different at 1% level (F .01 = 4.32).

During diapause, metabolism is at a very low level. A calculation from the data of McDonald and Brown (8) and Lejeune *et al.* (7) indicates that the rate of oxygen consumption during diapause is slightly less than 40 per cent of that of the newly-cocooned larva. As there is very little expenditure of energy by the diapausing eonymph, weight and lipid content remain more or less constant during this stage. Therefore it is possible to use these values as quantitative measures of the effects of restricted food intake and subsequent utilization of reserves for pre-diapause activity.

Table II presents a synopsis of the data pertaining to larval weights and lipid content for the laboratory reared material. The mean wet and dry weights and lipid contents of larvae of the various groups are significantly different and the variability within the groups is relatively small. Restriction of feeding is reflected quantitatively by marked diminution of size and reduction of lipid reserves.

Analysis of the data for lipid content expressed as per cent of wet weight shows that the variation between treatments is highly significant. In contrast to this, the group differences in lipid content expressed as percentage of dry weight and percentage of water content are not significant at the usually acceptable levels of 1 per cent or 5 per cent. The differences in percentage water content although relatively small are probably of physiological significance.

The percentage water content shows an increase with increasing extent of starvation. This increase in water content during starvation can be attributed to the accumulation of metabolic water concomitant with the metabolism of lipids and other reserves (2). The larvae of Group II although in a nearly fully-fed condition show a high percentage water content, apparently due to the retention of metabolic water produced during the initial three days of starvation. This ability of partially starved larvae to conserve metabolic water may aid them in resisting desiccation during the period spent in the cocoon.

The values for percentage lipid content and percentage water content of the fully-fed larvae are similar to those reported by Prebble (9) for the diapausing eonymphs of the European spruce sawfly, (*Diprion hercyniae* (Htg.)), which contained 35 per cent of dry weight, ether extractable lipid and 68.6 per cent water. Kozhantchikov (5) reported the following values for diapausing pre-

TABLE III

Weights and Lipid Content of Eonymphs of Partially-starved Larvae Expressed as Per Cent of Weights and Lipid Content of Fully-fed Controls

Group	Duration of feeding period as per cent of duration of control feeding period	Mean wet weight as per cent of control mean wet weight	Mean dry weight as per cent of control mean dry weight	Mean lipid content as per cent of mean lipid content of control
II	93	98.2	87.5	89.6
III	53	88.4	80.9	70.1
IV	32	75.1	49.5	37.6

pupae of the Tenthredinid *Croesus septentrionalis* L.: fat, 26 per cent of dry weight; and water content, 61 per cent of live weight.

In Table III the partially starved groups are compared, on a percentage basis, with the control group with reference to their wet and dry weights and lipid content. The group differences are best evidenced by their relative content of lipids. This value provides the most sensitive index of the relative degree of starvation.

Histological Appearance of Fat Body

Eonymphs from the various laboratory rearings were fixed in Allen's B-15 solution at 80°C. for 3 or 4 hours. Serial sections of whole larvae were cut at 9 μ and were stained with Heidenhain's iron-hematoxylin.

Fragments of fat body from the sheath of cells surrounding the mid-gut were dissected from representative larvae and stained for cytochemical differentiation of lipids by the Jackson procedure using Acetic-Carbol-Sudan III (3).

Progressive starvation is characterized by a decrease in the number and size of the fatty inclusions of the fat-body cells. This is illustrated in the accompanying photomicrographs of fat-body cells of eonymphs of fully-fed larvae (Fig. 1 and 2) and larvae which were fed for three days and then starved (Fig. 3 and 4).

PARTIAL STARVATION OF LARVAE IN FIELD POPULATIONS

The reduced size of the cocooned larvae is the most noticeable effect of partial starvation in field populations developing under conditions where the foliage supply is insufficient to support fully the larval population. This aspect of starvation was studied in a tamarack stand located near Telford in the Whiteshell Forest Reserve of Manitoba. At the close of the larval feeding period in late August 1952, cocoons were collected beneath three completely defoliated trees and one lightly defoliated tree. The diapausing eonymphs from these collections were weighed and analysed for lipid content. The data are summarized in Table IV. The eonymphs from the completely defoliated trees had significantly smaller mean wet and dry weights and lower mean lipid content than the eonymphs from the partially defoliated tree. There was no appreciable difference in the percentage variability of the larval wet weights for the two groups. The coefficient of variability for the larval wet weights was 16.7 per cent for larvae from the completely defoliated trees and 14.0 per cent for larvae from the partially defoliated tree.

Periodic collections of fully mature larvae were made from selected trees

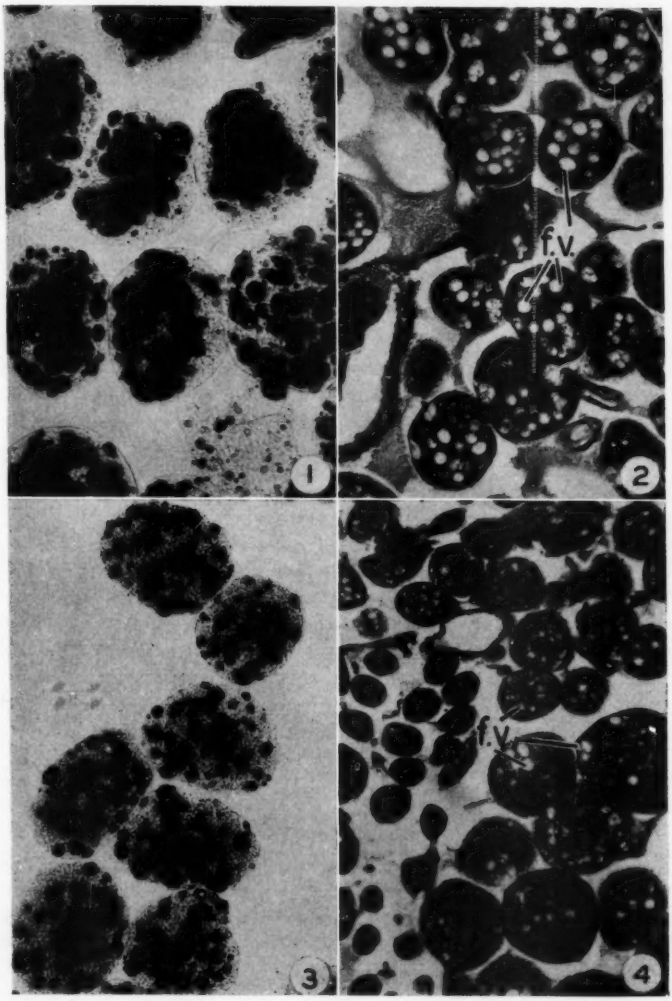


Fig. 1. Fat body cells from sheath surrounding mid-gut of diapausing eonymph of fully-fed larch sawfly larva showing the large number of fatty inclusions. Fixed in formalin and stained with Acetic-Carbol-Sudan III. (Cells somewhat flattened in mounting). X200.

Fig. 2. Section of diapausing eonymph of fully-fed larch sawfly larva showing fat body cells adjacent to mid-gut with numerous, large fat vacuoles (f.v.). Fixed in Allen's B-15 solution and stained with Heidenhain's iron haematoxylin. X200.

Fig. 3. Fat body cells from sheath surrounding mid-gut of diapausing eonymph of larch sawfly larva which had fed for three days during the fifth stadium. Showing the effect of starvation in reducing the number and size of the fatty inclusions. Fixed in formalin and stained with Acetic-Carbol-Sudan III. (Cells somewhat flattened in mounting). X200.

Fig. 4. Section of diapausing eonymph of larch sawfly larva which had fed for only three days during the fifth stadium, showing fat body cells adjacent to mid-gut. Compare with Fig. 2. Fixed with Allen's B-15 solution and stained with Heindenhain's iron haematoxylin. X200.

TABLE IV

Weights of Eonymphs From Cocoons Collected Beneath Completely-defoliated and Partially-defoliated Trees

Degree of defoliation	No. of trees sampled	No. of larvae weighed	Mean wet weight (mg.)	Mean dry weight (mg.)	Mean lipid content (mg.)	Water content per cent	Lipid content per cent
Completely defoliated	3	37	48.1	19.2	6.5	60.3	33.8
ca 50% defoliated	1	20	59.7	23.2	8.7	60.5	36.7
F	–	–	26.3*	17.9*	8.1*	–	–

*Significantly different at 1% level (F .01 = 7.12).

at progressive stages of defoliation to determine at what stage of defoliation restriction of foliage supply influences the size of the developing larvae. Collections were made by trapping the larvae, as they fell from the tree preparatory to cocooning, in funnel-traps. The trap consisted of a cloth funnel, measuring 2 by 2 feet at the mouth, at the apex of which there was a quart tin containing sphagnum moss. Larvae falling into the funnel burrowed into the moss to spin their cocoons. The trays were set out during the second week of July 1953, before any of the feeding larvae had entered the fifth stadium. The traps were examined at semiweekly intervals and the cocooned larvae removed. An ocular estimation of defoliation was made at the same time. The cocoons were then packed in moist moss and subsequently placed in cold storage. The following January the eonymphs were removed from their cocoons and weighed.

TABLE V

Wet Weights of Eonymphs From Cocoons Collected at Progressive Stages of Host Defoliation

Estimated per cent defoliation at time larvae matured	Number of eonymphs weighed	Mean wet weight of eonymphs (mg.)
10	6	57.6
10	8	62.6
20	67	60.3
30	44	60.9
40	22	51.6
50	39	60.2
70	2	59.0
80	11	54.6
90	19	60.7
90–100	28	47.5

In Table V the combined data on weights of larvae collected in eight traps are grouped according to the degree of defoliation at the time of collection. The numbers of larvae weighed are not necessarily proportional to the number actually collected at any particular stage of defoliation. It appears from these data that starvation does not become a significant factor until the defoliation exceeds 90 per cent.

In a further study of the effects of partial starvation, two random collections of cocoons were made in the fall of 1953, one from an area where larval starvation had been significant and one where the larvae had had an adequate supply of foliage. The former collection was made in the Duck Mountain Forest Reserve, north of Grandview in western Manitoba, where heavy defoliation by the larch sawfly has been recorded for a number of years and where complete defoliation occurred in 1953. The other collection was made near Pierceland in northwestern Saskatchewan where the larch sawfly has just recently attained a high population level and where defoliation was light in 1953.

Data relating to the weights and lipid content of eonymphs from these cocoon collections are summarized in Table VI. There is a marked difference in the size of the larvae from the two areas. The larvae which developed under conditions of adequate foliage supply are relatively uniform in size compared with the partially starved larvae from the Duck Mountain collection. The lipid content of the larvae from the latter population shows a particularly large percentage variability.

THE EFFECT OF PARTIAL STARVATION ON REPRODUCTIVE CAPACITY

Measurement of Reproductive Capacity

Of the adults examined the maximum development of the female gonads was exhibited by vigorous specimens emerging from cocoons which were collected near Pierceland, Saskatchewan, in 1953. The following description of the ovaries refers to the state of development exhibited by an average specimen from this population.

The ovary consists of twenty ovarioles of the polytrophic type. A well-developed ovariole, at the time of adult eclosion, contains two fully-formed oocytes, complete with chorions; one near-mature oocyte of almost full size but lacking a chorion; and two or three very small immature oocytes. Those oocytes which lack a chorion have a cluster of nurse cells located proximally.

TABLE VI

Weights and Lipid Contents of Eonymphs From Starved and Non-starved Field Populations

Collection locality	Stand defoliation	Number of eonymphs weighed	Wet weight (mg.)			Dry weight (mg.)			Lipid content (mg.)		
			Mean	S.E. ±	Coefficient of variation	Mean	S.E. ±	Coefficient of variation	Mean	S.E. ±	Coefficient of variation
Pierceland, Saskatchewan	lightly defoliated	50	73.0	1.2	11.6%	28.7	0.5	12.3%	8.1	0.2	18.5%
Duck Mountain Forest Reserve, Manitoba	completely defoliated	50	46.6	1.3	19.7%	16.3	0.6	25.9%	3.1	0.2	51.5%
% difference	–	–	36.2	–	–	43.2	–	–	61.7	–	–

B&Z Library

TABLE VII

The Reproductive Capacity of Larch Sawfly Adults as Determined by Oviposition Tests and Dissection

Series	Number of Adults	Adult weight (mg.)		Number of mature oocytes (+eggs)	
		Mean	S.E.	Mean	S.E.
Oviposition	25	47.6	±0.9	71.9	±3.8
Dissection	17	43.3	±1.2	89.1	±3.9
F		10.49*		9.48*	

*Significantly different at 1% level (F .01 = 7.29).

Reproduction in the larch sawfly is by obligatory parthenogenesis (11). As there is no need for fertilization of the eggs and since the imago is capable of oviposition almost immediately after eclosion, the measurement of reproductive capacity is greatly simplified. For purposes of comparison, fecundity was measured in two ways: 1) by means of oviposition tests; 2) by adult dissections. In the oviposition tests female adults were kept for one day after eclosion to allow for discharge of the meconium and they were then weighed. Next they were placed, singly, in cages and each was provided with three to five fresh tamarack shoots for oviposition. The shoots were inserted in water-filled vials to keep them fresh. Following death, the adult was dissected and the residual oocytes were counted. In the dissection determinations the adults were weighed one day after emergence, dissected and complete counts of the mature and immature ova made. To facilitate examination the ovaries were treated with Sudan III, which stained the immature ova heavily and differentiated them from the nurse cells. Fully developed ova, complete with chorion, did not take up the stain readily.

The data from these tests are presented in Table VII. The figures for the oviposition group include the number of eggs oviposited plus the number of mature and near-mature oocytes determined by dissection after death. The count for the dissection group consists of the total number of mature plus near-mature ova. The mean number of oocytes for the adults of the dissection group was significantly greater than that of the oviposition group even though the adults of the latter group had a slightly greater mean weight. This indicates that the small immature oocytes that are present at eclosion do not mature during adult life and that the determination of fecundity by dissection of newly eclosed adults is not an underestimation as it would be if such post-emergence maturation did occur.

Some of the adults in the oviposition series lived seven days and most of them lived for at least four days. It is possible that during this period some oosorption of mature oocytes occurred, thus accounting for the lower mean reproductive capacity of adults of this group. No visual evidence of oosorption was noted however.

Adult live weight and reproductive capacity, i.e. the number of mature plus near-mature oocytes, were closely correlated. The correlation coefficient for the dissection group was +0.7819 and for the oviposition group +0.4225. Both

TABLE VIII

Reproductive Capacity of Females from Starved and Non-starved Field Populations

Source	No. of females dissected	Adult live weight (mg.) (x)		No. of mature oocytes per female (y)		Correlation coefficient	Regression equation for estimating reproductive capacity from adult weight
		Mean	S.E. ±	Mean	S.E. ±		
Pierceland, Sask. (1953)	15	42.9	2.5	66.5	5.3	+.906	$y = 1.9383\ x - 16.6461$
Duck Mountain Forest Reserve (1953)	15	27.1	1.8	39.5	3.9	+.898	$y = 2.4615\ x - 27.2562$

of these coefficients were highly significant. The higher correlation shown by the dissection group lends support to the reliability of this method of determining reproductive capacity.

The Comparative Reproductive Capacity of Partially-starved and Non-starved Populations

Reeks (10) has reported a very marked and progressive decline in the reproductive capacity of adults from a given area, during the final six years, (1937-1942), of an outbreak of the larch sawfly in the Maritime Provinces. He considered that this reduction may have been related to partial starvation. No comparable data are as yet available in relation to the present outbreak in the Prairie Provinces. The effect of starvation on reproductive capacity was studied by comparing the fecundity of adults emerging from cocoons collected in 1953 at Pierceland, Saskatchewan, and in the Duck Mountain Forest Reserve, north of Grandview, Manitoba. These are the two populations for which data on larval weights were presented earlier in this paper. Reproductive capacity was determined by dissection. The data are summarized in Table VIII.

The mean reproductive capacity of the individuals from the starved population was over 40 per cent less than that of the members of the non-starved population. For each population there was a strong positive correlation between adult weight and the number of mature oocytes. The regression equations for determining reproductive capacity from adult weights are given for both populations. The equation derived for the more fecund population would give reliable results if used to determine the reproductive capacity of the starved population. However, the equation derived from the data for the starved population could not be used reliably in determining the reproductive capacity of the more fecund population due to the divergence of the two regression lines in the region of the larger adults of the latter population. Prebble (9) has pointed out the pitfalls that may be encountered in the indiscriminate application of such regression equations for the determination of the fecundity of populations other than those from which they were derived.

As the two groups of adults exhibited a marked contrast in mean reproductive capacity, it was considered that this difference might be reflected in the mean size of the egg clusters deposited by adults of the two populations. To investigate this possibility, a collection of shoots, in which eggs had been laid, was

TABLE IX

Egg Cluster Size in Starved and Non-starved Field Populations

Location	Number of trees sampled	No. of curled shoots examined	Length of curled shoots (mm.)		Mean number of eggs per shoot	
			Mean	S.E.	Mean	S.E.
Pierceland, Saskatchewan	5	28	44.4	±2.6	15.5	±1.3
Duck Mountain Forest Reserve, Manitoba	7	77	49.8	±2.4	18.5	±1.3

made in each of the two areas concerned, at the close of the oviposition period in 1954. The data obtained are summarized in Table IX.

There was no appreciable difference in the mean number of eggs per shoot. The distribution of egg cluster size in each population was also closely similar although the size of the sample from the Pierceland area was too small to permit generalization in this respect.

DISCUSSION AND SUMMARY

Partial starvation in larch sawfly larval populations is symptomatic of prolonged outbreaks and cocooned larvae in such populations are sub-normal in size and deficient in lipid reserves. Individual starved larvae can be readily recognized on examination of their fat body cells, when stained for cytochemical differentiation of lipid. The cells of fully-fed larvae are heavily laden with large fat inclusions while the fat globules in the cells of partially-starved larvae are disperse, smaller in size, and usually peripheral in position.

Qualitative nutritional differences may result from repeated defoliation of the host trees. Fully-fed larvae from a prolonged outbreak area in eastern Manitoba were, on the average, 18 per cent lighter than fully-fed larvae from a newly-established population near Pierceland, Saskatchewan. The difference in the lipid content of the two groups of larvae was negligible. It is possible that the weight difference was due to a qualitative difference in the foliage of the two areas related to their contrasting defoliation history.

Partial starvation of larvae results in a reduction of adult reproductive capacity. As outbreak populations reach the stage where the foliage production of the host tree declines beyond the point where it can support the population, there will be a concomitant decrease in mean reproductive capacity. Annual fluctuations in mean reproductive capacity will occur at this stage dependent on annual variations in population density as determined by mortality factors. Starvation will always be imminent however, because of the restricted foliage supply of the host trees. Mean individual reproductive capacity is not likely to be reduced to the point where it will be reflected in a marked decline in mean egg cluster size. Egg cluster size is probably more closely related to phenological and tree-growth factors. The mean number of oviposition sites utilized per adult will be reduced by starvation but this in itself cannot be related to the influence of starvation without consideration of the density of the adult population.

ACKNOWLEDGMENTS

The writer wishes to express his appreciation to colleagues of this laboratory for their critical review of the manuscript and to members of the staff of the

Forest Insect Survey for making some of the field collections. Special thanks are due to Mr. H. Weisman, Department of Zoology, University of Manitoba for taking the photomicrographs.

REFERENCES

1. Bloor, W. R. 1943. Biochemistry of the fatty acids and their compounds, the lipids. Reinhold Publ. Corp., New York.
2. Fraenkel, G. and Peh-I. Chang. 1954. Manifestations of a vitamin B_T (Carnitine) deficiency in the larvae of the meal worm *Tenebrio molitor* L. *Physiol. Zool.* 27: 40-56.
3. Glick, D. 1949. Techniques of histo- and cytochemistry. Interscience Publishers, Inc., New York.
4. Heron, R. J. 1951. Notes on the feeding of larvae of the larch sawfly, *Pristiphora erichsonii* (Htg.) (Hymenoptera: Tenthredinidae). *82nd Ann. Rep. Entomol. Soc. Ont.* 67-70.
5. Kozhantschikov, I. W. 1938. Physiological conditions of cold-hardiness in insects. *Bull. Ent. Research.* 29: 253-262.
6. Lejeune, R. R. 1951. Some ecological factors governing populations of the larch sawfly, *Pristiphora erichsonii* (Htg.) *Can. Ent.* 83: 152-156.
7. Lejeune, R. R., W. H. Fell, and D. P. Burbidge. 1955. The effect of flooding on development and survival of the larch sawfly, *Pristiphora erichsonii* (Tenthredinidae). *Ecology* 36: 63-70.
8. McDonald, S., and A. W. A. Brown. 1952. Cytochrome oxidase and cyanide sensitivity of the larch sawfly during metamorphosis. *83rd Ann. Rept. Entomol. Soc. Ont.* 30-34.
9. Prebble, M. L. 1941. The diapause and related phenomena in *Gilpinia polytoma* (Hartig) IV. Influence of food and diapause upon reproductive capacity. *Can. J. Res. D.* 19: 417-436.
10. Reeks, W. A. 1954. An outbreak of the larch sawfly (*Pristiphora erichsonii* (Htg.)) (Hymenoptera: Tenthredinidae) in the Maritime Provinces and the role of parasites in its control. *Can. Ent.* 86: 471-480.
11. Smith, S. G. 1955. Cytogenetics of obligatory parthenogenesis. *Can. Ent.* 87: 131-135.

(Received August 25, 1955)

Frass-drop Studies of Larvae of *Neodiprion americanus banksianae* Roh. and *N. lecontei* (Fitch) (Hymenoptera: Diprionidae)[1]

By G. W. Green[2] and A. S. deFreitas[3]

INTRODUCTION

Among others, Schwerdtfeger, 1931, Gosswald, 1934, and Morris, 1949, have used frass-drop samples as indirect measurements of the density of forest insect populations with some success. The method has also been used to assess the effects of various insecticides on the feeding of treated larvae (Rhumbler, 1929; Schwerdtfeger, 1930) and to study the influence of weather upon the feeding and development of forest insects (Monro, 1935).

The rate of feeding during different kinds of weather provides a measure of the effect of meteorological conditions on insect activity, but, in colonial forms especially, it is often difficult to decide by visual observation whether a colony is feeding heavily, moderately, or lightly. Frass-drop measurements appear to be a simple solution to the problem. Furthermore, once the rate of frass-drop under different conditions has been established for a known number of larvae of each stadium, it would seem a simple matter to use these data as the basis for an accurate method of sampling population densities. Also, since frass-pellet size is directly related to larval instar in most species, it should not

[1]Contribution No. 227, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada.
[2]Forest Insect Laboratory, Sault Ste. Marie, Ontario.
[3]Macdonald College, Quebec.

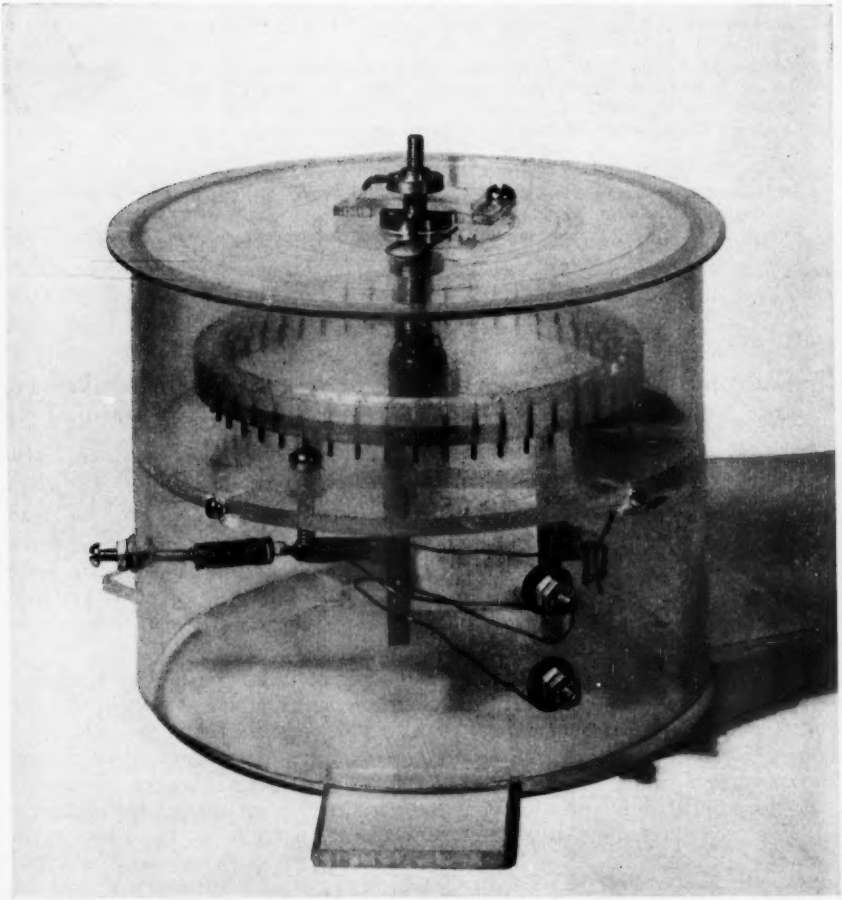
be difficult to establish the composition of the population by instars at the time of sampling.

These points were investigated by studying two species of pine sawflies, *Neodiprion americanus banksianae* Roh. and *N. lecontei* (Fitch), in the laboratory and in the field. These studies indicate certain pitfalls in the technique that make it less satisfactory for measuring population density than might otherwise be expected. It is the purpose of this paper to discuss these difficulties and to point out some of the errors that have been foreseen by Morris (1949) but appear not to have been mentioned in the literature.

METHODS AND MATERIALS

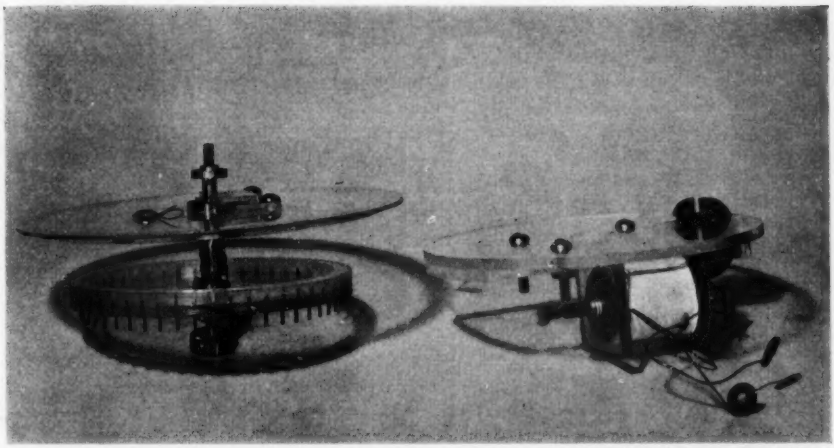
Experimental Insects

Eggs and larvae of *N. a. banksianae* were collected from jack pine, *Pinus banksianae* Lamb., in Bright Township near Iron Bridge, Ontario. Those of



Photograph by D. C. Anderson

Fig. 1. The coprometer minus its collecting disc. Three of these units were connected in parallel through the same timing switch.



Photograph by D. C. Anderson

Fig. 2. Working parts of coprometers used in frass-drop studies. The retaining post and the solenoid are shown at the right, and the escapement disc and drive spring at the left.

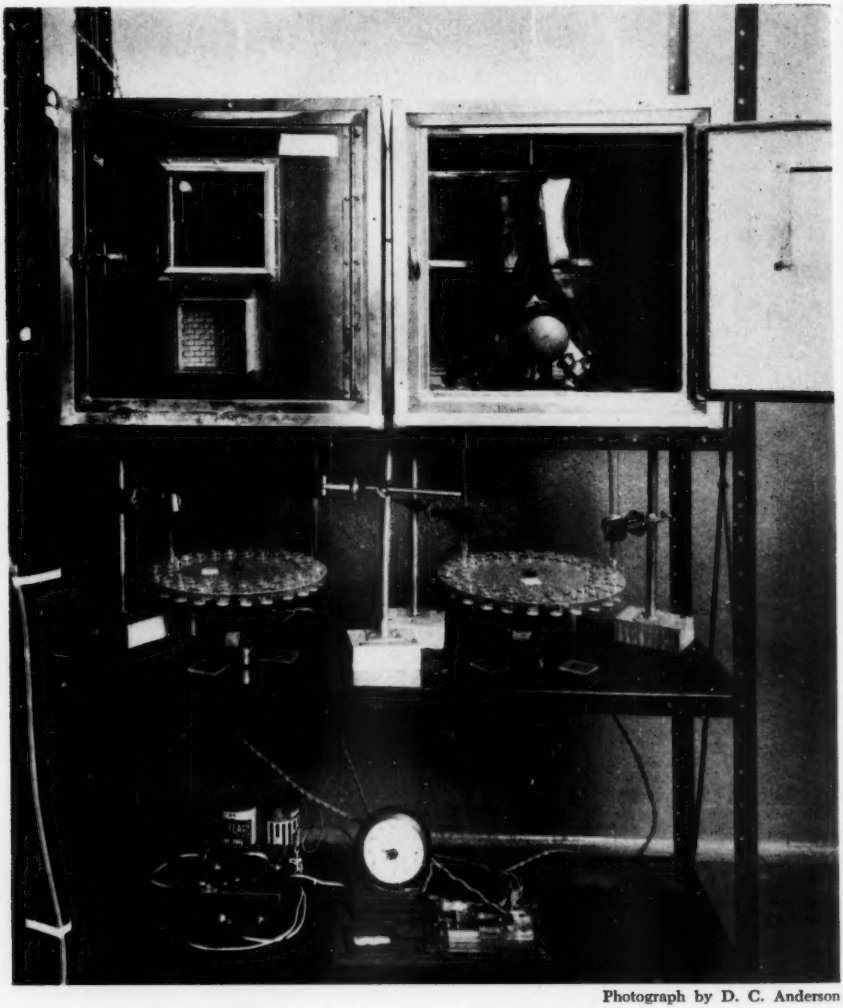
N. lecontei were collected from red pine, *Pinus resinosa* Ait., in Welk Township near Goldenburg, Ontario. Branches containing eggs were set up in the laboratory with the cut ends immersed in water and larvae that had already eclosed were placed on new foliage. After the head capsules of first-instar larvae had darkened in the laboratory, those for use in the field were transferred to host trees in the study area.

Coprometers

Many types of coprometers have been employed by various workers in the past, and some of these have been described in an earlier paper (Green and Henson, 1953). As a direct result of the new coprometer described in that paper, a modified model of much simpler design and greater efficiency, was constructed for use in these studies. This apparatus, minus its collecting disc, is shown in Fig. 1; a breakdown of its parts in Fig. 2. A solenoid, with the plunger hooked to the retaining post, replaces the bulky horseshoe magnet used in the earlier model. The escapement disc has been simplified to a single row of posts instead of the double row of teeth in the prototype. Activation of the solenoid is accomplished through a simple timing switch. An arm connected to the minute shaft of an alarm clock tips a mercury switch once an hour to close a 12-volt circuit. The addition of extra arms provides intervals of less than one hour. A current of 12 volts is sufficient to operate three coprometers wired in parallel through the same switch and to supply sufficient reserve power for them to function through minor mechanical difficulties, such as sticking retaining posts or sluggish solenoids. Six coprometers were constructed; three for controlled experiments and three for use under field conditions.

Laboratory Experiments

Horsfall cabinets were equipped with individual temperature controls and were split up as shown in Fig. 3 so that duplicate experiments at the same temperatures could be run. Since it had been shown earlier (Green, 1954) that larvae of both species prefer regions of low humidity, no humidifiers were placed in the cabinets and the heating units kept the air quite dry. Although



Photograph by D. C. Anderson

Fig. 3. Coprometers set up to collect frass during paired experiments at the same temperature in the laboratory. The timing switch used in these studies is shown in the lower portion of the photograph.

preliminary experiments indicated that temperature was the most important meteorological factor influencing the rate of frass-drop by both species, light was kept constant throughout the experiments. Collecting discs of coprometers used in the laboratory contained two rows of collecting bins, one row to collect frass from insects in one side of the cabinet, and one from the other.

Since studies in the laboratory were designed to demonstrate inter-instar differences in the rate of frass-drop, larvae were taken from the laboratory stock the day after moulting to the instar to be tested. Groups of 20 larvae were placed upon freshly cut foliage with the cut ends immersed in water. When

they had formed compact feeding groups under room conditions, they were placed in the cabinets. Frass-drop collections made during the first three hours of any test were rejected because larvae sometimes shifted their feeding sites after being placed in the cabinets and they needed some time to become regrouped. In general, collections were made for 12 hours at each constant temperature (±1.0°C.). Occasionally, a larva left the cluster and crawled on the walls of the cabinet or fell from the foliage into the frass bins. When this occurred, frass-drop values were adjusted to the equivalent of 20 larvae by an appropriate conversion factor.

Frass-pellet counts were used throughout since volumetric or weight measurements of such small samples as the hourly collections provided are subject to relatively large errors. All frass measurements are given in terms of the working unit of 20 larvae.

Field Experiments

Field studies were carried out at the Point aux Pins Insectary of the Forest Insect Laboratory just west of Sault Ste. Marie, Ontario, during the summer of 1954. Standard Stevenson screen weather records were augmented by hourly observations of wind speed and direction, observations of the type and amount of cloud and precipitation, solar radiation measurements made with a General Electric radiation meter, and other notes of events of particular interest. Temperature measurements for correlation with larval activity were made with No. 24 and No. 30 copper-constantan thermocouples recording on a Brown Multiple Point potentiometer. This instrument recorded temperatures at each site at six-minute intervals. Tests indicated that exposed bark temperatures were better correlated with larval activity than were shielded or unshielded air temperatures. Consequently, bark temperature measurements were made on the upper surfaces of the branches as close as possible to the feeding site of each colony.

Counts of larvae over each coprometer were made daily and recorded in terms of the relative numbers of each instar present. Thirty-five to 80 larvae were maintained over each coprometer throughout the developmental period.

RESULTS

Laboratory Investigations

N. a. banksianae

Frass-drop of *N. a. banksianae* larvae at different constant temperatures is illustrated in Fig. 4, where freehand curves are drawn through the means and one standard deviation of the frass-drop at each temperature level. This figure shows that maximum rates of frass-drop by each instar tested occurred between 31 and 33°C. and that no frass was dropped above 37-39°C. As evidenced by the spread of the means and their standard deviations at each temperature level, later instars exhibited more consistent rates of frass-drop than did earlier instars. Simple calculations from these data show that maximum rates of frass-drop per larva per hour decreased from 6.4 pellets for instar II to 4.9 pellets for instar V, a decrease of 23%. This, of course, does not mean that there is a corresponding decrease in feeding rates through the instars because pellet size increases rapidly as the larvae develop.

N. lecontei

Preliminary investigations in 1953 showed that larvae of *N. lecontei* dropped different amounts of frass at a constant temperature when fed foliage of different ages. Two tests in 1954 with fourth- and fifth-instar larvae proved that these differences were highly significant (Table I). Larvae feeding upon new foliage dropped up to 32% more frass than larvae feeding upon old foliage.

R.A.F. library

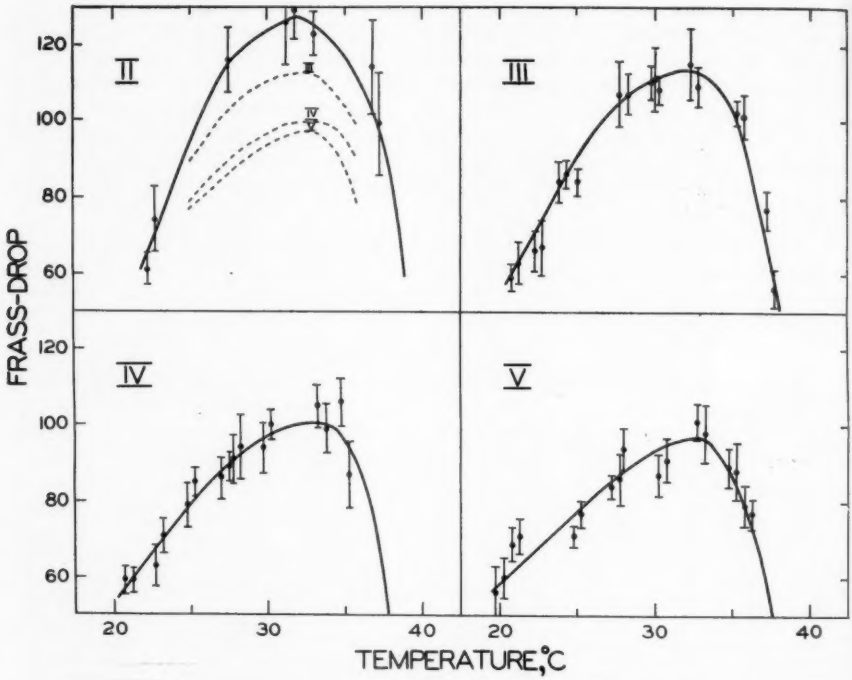


Fig. 4. Inter-instar comparisons of frass drop from larvae of *N. a. banksianae* at constant temperatures in the laboratory. Frass-drop values are the mean number of pellets dropped per hour by 20 larvae and are based on 12-hour collection periods. The fine lines through the means represent one standard deviation.

This complication was not encountered with *N. a. banksianae* because at the time the new foliage of jack pine had not elongated enough for the larvae to feed upon it. In *N. lecontei*, however, the introduced error was of sufficient magnitude to necessitate removing new foliage from the shoots used in laboratory studies.

Frass-drop of *N. lecontei* larvae at different constant temperatures is illustrated in Fig. 5. As in *N. a. banksianae*, maximum rates of frass-drop occurred between 31 and 33°C. for all instars tested, and frass-drop ceased between 37 and 39°C. Similarly, more consistent rates of frass-drop occurred during the later instars. In *N. lecontei* maximum rates of frass-drop per larva per hour decreased from 5.8 pellets during instar III to 3.5 pellets during instar VI, a decrease of 40%. The general shapes of the frass-drop: temperature curves of this species were very similar to those of *N. a. banksianeae*.

Field Investigations

Factors such as wind (within reasonable limits), relative humidity, and light seemed to have little effect on the frass-drop of either of the species studied. Solar radiation, insofar as it affected the body temperature of larvae (Green, unpublished data), proved important, but since it affected bark temperature in much the same way, it was not considered as a separate factor affecting the rate of frass drop. Heavy rain halted feeding of all instars of both species, whereas

light rain or drizzle seemed to have no effect although no frass-drop measurements could be made during these periods because the wet frass stuck to the sides of the funnels and never appeared in the collecting bins until the funnels had dried after the rain.

TABLE I

Comparison of the hourly frass drop from colonies of 20 larvae of *N. lecontei* feeding upon either current or previous year's foliage at two different temperatures

	N. lecontei IV 32.5°C.		*N. lecontei* V 25.5°C.	
	New foliage	Old foliage	New foliage	Old foliage
n	12	12	12	12
$\bar{x}$	122.5	91.6	88.3	75.7
$s\bar{x}$	1.47	1.04	1.25	1.39
t	11.58		6.75	
P	< 0.001		< 0.001	

Where n = number of hours of collection, $\bar{x}$ = mean hourly frass-drop, and sx = standard of error of the mean

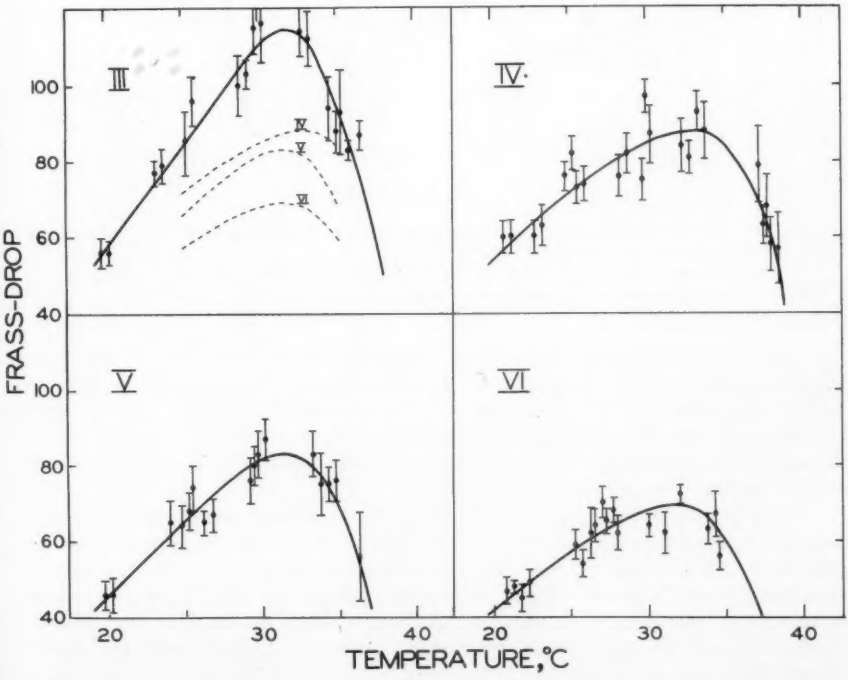


Fig. 5. Inter-star comparisons of frass drop from larvae of *N. lecontei* at constant temperatures in the laboratory. Frass-drop values derived as in Fig. 4.

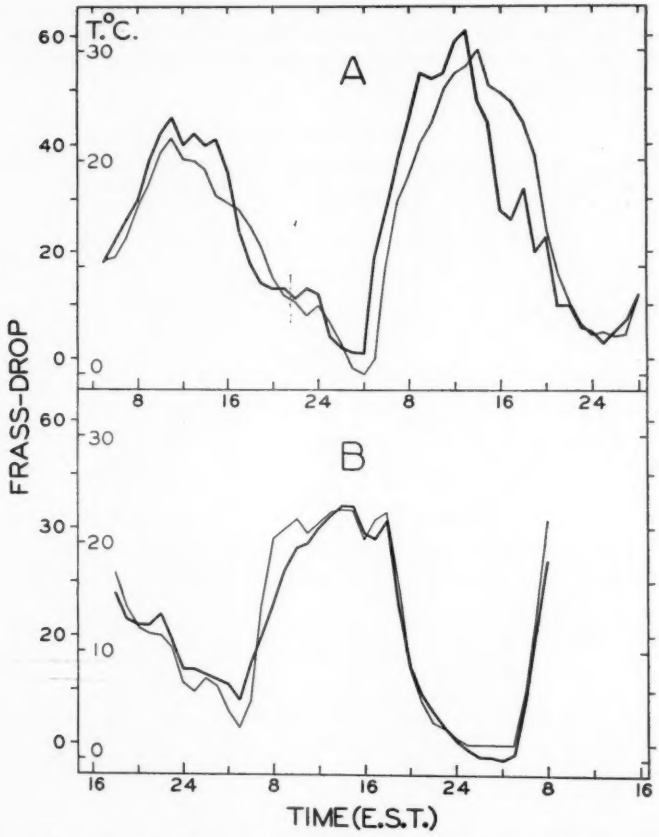


Fig. 6. The relationship between frass drop (heavy lines) and bark temperature (fine lines) on clear days in the absence of parasites.
A. Fourth- and fifth-instar larvae of *N. a. banksianae* on June 27 and 28, 1954.
B. Fifth-instar larvae of *N. lecontei* on August 18 and 19, 1954.

Temperature affected the rate of frass-drop more than any of the other meteorological factors. Figures 6A and B illustrate the relationship between bark temperature and frass-drop that may be expected during days characterized by relatively smooth temperature fluctuations and no disturbing external stimuli. A very close relationship exists between frass drop and exposed bark temperature at the feeding sites during such periods.

Such good relationships could only be demonstrated during relatively few days throughout the summer, because two species of parasites were nearly always present at the colonies. They had a marked depressive effect on the rate of frass-drop from the larvae (Figs. 7A and B), completely destroying the normal temperature: frass-drop relationship. Although their presence at the colonies produced much the same result, the manner of attack differed with the species of parasite.

The method of attack of the dipterous parasite, *Spathimeigenia erecta* Ald. was especially interesting. This parasite actually herded larvae from their feeding

positions on the needles into compact groups near the feeding site. It accomplished this by darting at the larvae so that they first exhibited a violent alarm reaction that spread through the colony and then retreated from the needles to cluster near the feeding site. When the larvae had formed this group, the fly darted rapidly back and forth above them. Oviposition could not be seen because the fly moved so quickly. When this parasite was present, the entire colony was disrupted and frass-drop was markedly affected. The fly was present throughout the larval development of both species but seemed to attack the larvae most during and after the third instar.

The hymenopterous parasite, *Exenterus platypes* Cushman attacked the larvae in an entirely different way. This species could fly to the colony and alight near it without causing any alarm reaction. Once near the colony, it proceeded to crawl towards the larvae very slowly. When it reached the larvae, it moved slowly over their backs, still without noticeably disturbing them. However, once oviposition began, larvae became excited and moved away from the feeding

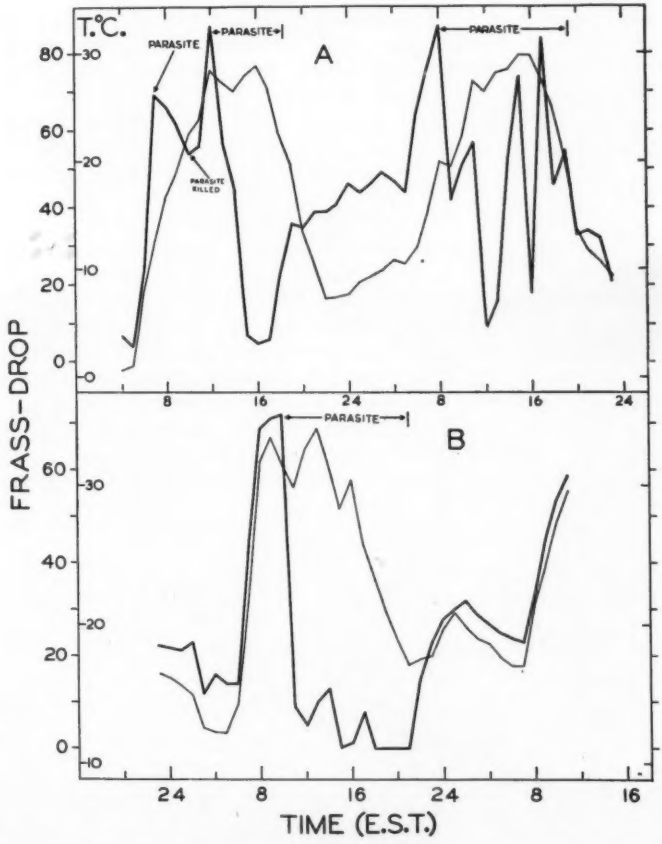


Fig. 7. The effect of *Spathimeigenia erecta* Ald. on frass drop from larvae of (A) *N. a. banksianae* and (B) *N. lecontei*. Frass drop is represented by the heavy line and bark temperature by the light line. The effect of *Exenterus platypes* Cushman was much the same.

site. The presence of this parasite thus took longer to affect the whole colony, but the end result was the same. This parasite, too, seemed to attack more often after larvae had reached the third instar.

Both species were present around colonies of *N. a. banksianae* and of *N. lecontei*. Attacks such as those described above always occurred during daylight after temperatures had risen in the morning, often persisting for as long as eight hours and greatly disrupting normal frass-drop during this period. When parasites left, larvae resumed feeding and, in some instances, fed for short periods, at a more accelerated rate than normal for the prevailing temperature.

Throughout the summer, sufficient frass-drop: temperature measurements were accumulated in the absence of parasites for correlation of the regression of frass-drop on temperature. It is unfortunate that temperatures beyond the maximum for frass-drop were seldom encountered in the field, so that no decrease in frass-drop as temperatures increased above maximum could be demonstrated. However, a fairly broad range of temperatures was experienced with some interesting results.

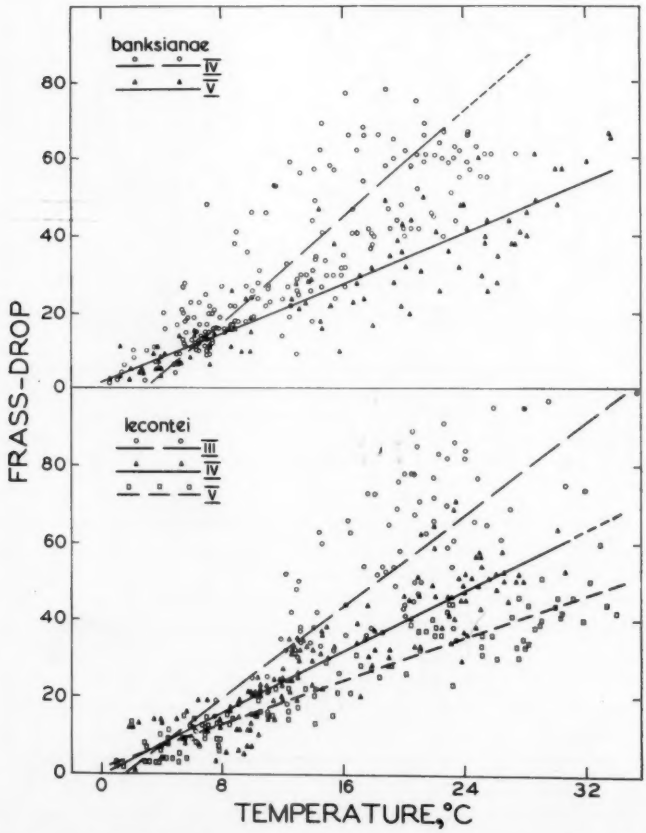


Fig. 8. Regression of frass drop on bark temperature for larvae of *N. a. banksianae* and *N. lecontei* in the field on clear days in the absence of parasites. For correlation coefficients see Table II.

Correlations of frass-drop with temperature were obtained in the field (Fig. 8) and the general relationships found in the laboratory were found to hold. As in laboratory tests, both the rate and variability of frass-drop decreased during successive instars. Frass from the earlier instars could not be collected readily in the field because the fine frass pellets tended to stick to any irregularities in the funnel sides or fell through the nylon mesh floors of the collecting bins.

When laboratory and field results are compared, several anomalies are evident. Since temperature: frass-drop values in the laboratory seem to follow a straight line relationship at the lower end of the temperature scale (Figs. 4 and 5), rates of frass-drop with temperature were calculated between 20 and 28°C., for larvae of *N. a. banksianae*, and between 20 and 30°C., for larvae of *N. lecontei*. These values are compared with field frass-drop rates in Table II. This table shows that field rates were always lower than those established in the laboratory and that a constant ratio between laboratory and field results did not exist through successive instars. Instead, ratios between laboratory and field frass-drop rates tended to increase as the larvae developed until field rates were less than one-half laboratory rates by the time both species had reached the fifth instar.

Table II compares the rate of frass-drop only and does not indicate the differences in the actual amount of frass dropped by larvae at comparable temperatures in the laboratory and in the field. Table III compares the mean frass-drop by 20 larvae at temperatures of 20 and 30°C in the laboratory and in the field. This table shows that the only comparable results between laboratory and field were for fourth-instar larvae of *N. a. banksianae* and that all other comparisons showed large discrepancies.

DISCUSSION

Frass-drop measurements were of limited value in studying the effects of meteorological factors upon the feeding activity of the two sawflies when the effects of parasites could be eliminated. Unfortunately, temperatures sufficiently high to discourage feeding never occurred during days when parasites were absent, so that a complete temperature:feeding-activity relationship was not established. It was found, however, that larvae of both species fed from about 6°C. to at least 32°C. in linear relation to bark temperature at the feeding site. Although Fig. 8 indicates that some frass is dropped at temperatures below 6°C., this does not mean that larvae were actually feeding at these low temperatures. Frass that appeared in the collecting bins at temperatures below 6°C. averaged

TABLE II

Comparison of the rates of frass drop from larvae of *N. a. banksianae* and *N. lecontei* in the laboratory and in the field at temperatures below the maximum for frass drop

	Laboratory	Field	Ratio
banksianae IV	4.69 (±.9672)	3.43 (±.8554)	1.37
banksianae V	3.33 (±.9132)	1.64 (±.9108)	2.03
lecontei III	5.50 (±.9813)	3.16 (±.8313)	1.42
lecontei IV	2.89 (±.8426)	1.98 (±.8806)	1.46
lecontei V	3.58 (±.9603)	1.42 (±.9462)	2.53

The bracketed numbers beside the rates are the correlation coefficients in each case.

TABLE III

Comparison of the mean number of pellets dropped by 20 larvae of *N. a. banksianae* and *N. lecontei* at two different temperatures in the laboratory and in the field.

	20°C.			30°C.		
	Lab'y	Field	% diff.	Lab'y	Field	% diff.
banksianae IV	54	59	9.2	97	93	3.2
banksianae V	59	34	42.4	94	50	46.9
lecontei III	58	56	3.5	110	89	19.1
lecontei IV	54	39	27.8	85	59	30.6
lecontei V	46	30	34.8	82	44	46.3

less than one-half pellet per larva per hour, and this could result from slow elimination of frass already in the posterior part of the alimentary tract, or from frass already eliminated but stuck to the foliage and eventually dislodged.

Laboratory results indicate a maximum frass-drop rate for all instars tested of both species at approximately 32°C. with complete cessation near 38°C. However, exactly how much these laboratory results can be relied upon in interpreting field behaviour is questionable since it has been shown that laboratory and field rates do not correspond well. Secondary factors affecting frass-drop rates were either absent or held rather constant in the laboratory but were quite variable in the field as evidenced in the scatter of points around the regression lines in Fig. 8. Although the effect of any one of these secondary factors may be quite small, a combination of them could exert a substantial influence on frass drop, and until these are well understood, interpretation of field behaviour on the basis of temperature frass-drop studies performed in the laboratory is subject to error.

It does not seem feasible to use frass drop as an indirect means of estimating population densities accurately in these species. Disturbing stimuli, such as parasites, completely disrupt the normal temperature:frass-drop relationship and introduce errors the degree of which cannot be measured under natural conditions. The effect of parasites may be felt long after the parasites have left the colony. It has been observed that larvae sometimes drop more frass than would be expected at the prevailing temperature for a short period after the resumption of feeding following parasite attack, but the general rule was that less frass was dropped by larvae in the field than by larvae in the laboratory at comparable temperatures, and that these differences increased through successive instars. This may be a result of acclimation to low nocturnal temperatures in the field, but it is also quite possible that it is partly an effect of parasites developing inside the larvae. Thus, population density estimates from frass-drop measurements taken in the field and compared with laboratory results would tend to make the estimates too low.

Differences in the rate of frass drop by larvae of *N. lecontei* feeding upon old and new foliage could also introduce a sizeable error into estimates of population density by the frass-drop method. It would be difficult or impossible to estimate accurately the percentage of larvae feeding upon either type of foliage so that no correction factor could be applied. In the instance tested,

an error of up to 32% could be added to other sources of error attendant on the method.

Frass-drop methods, therefore, seem best suited to studying the effects of physical factors upon the feeding activity of test colonies where parasite attack may be controlled, and where the instances of feeding upon old or new foliage can be observed and recorded. Since frass-pellet size is usually directly related to larval instar, frass-drop samples would give an indication of the stage of development of natural populations on trees too tall for visual checks. The value of frass-drop measurements from the same sites year after year in following population trends (Morris, 1949) cannot be disputed, but their application in more detailed studies is dangerous, and at least for the two species here studied, very unreliable.

SUMMARY

1. Frass-drop studies were carried out on larvae of *N. a. banksianae* and *N. lecontei* in the laboratory and in the field using coprometers of an improved design.
2. Temperature appears to be the most important meteorological factor affecting the feeding rates as measured by frass drop. Larvae of all instars tested of both species feed between approximately 6 and 38°C., with a maximum of approximately 32°C.
3. The presence of parasites seriously hampered studies under field conditions by completely disrupting feeding continuity of the colonies. Larvae in colonies visited by parasites drop less frass than undisturbed larvae presumably as a result of being parasitized.
4. Larvae of *N. lecontei* drop more frass when feeding upon the current year's foliage than do larvae feeding upon the previous year's. At 35.5°C., this difference amounted to 32% of the mean frass drop of larvae on old foliage.
5. Laboratory and field results agree well only in the earliest instar in which comparisons could be made, the former always being higher. The difference may be due to acclimation or parasitism or both.
6. Frass-drop measurements are of value in studying the effects of meteorological factors on the feeding activity of the two species studied, providing parasites can be controlled. They are also useful in estimating what development stages comprise populations on trees too high for visual checks and in following population trends. Extension of the frass-drop method to estimates of population density is subject to great errors.

ACKNOWLEDGMENTS

The authors wish to thank W. G. Wellington of the Forest Biology Laboratory, Victoria, B.C. for helpful advice during the study and during the preparation of the manuscript. We are also grateful to R. M. Belyea and other members of the staff of the Forest Insect Laboratory, Sault Ste. Marie, Ontario, for critical reading of the manuscript. Mrs. Stanley Buchanan and D. I. West assisted in the abstraction of much of the data and in the preparation of the figures.

REFERENCES

Gosswald, K. 1934. Uber die Frasstätigkeit von Forstschädlingen unter dem Einfluss von Altersunterscheiden und der Einwirkung verschiedner Temperature und Luftfeuchtigkeit und ihre praktische und physiologische Bedeutung. *Z. angew. Ent.* 21: 183-332.

Green, G. W. 1954. Humidity reactions and water balance of larvae of *Neodiprion americanus banksianae* Roh. and *N. lecontei* (Fitch) (Hymenoptera: Diprionidae). *Canad. Entom.* 86(6): 261-274.

Green, G. W., and Henson, W. R. 1953. A new type of coprometer for laboratory and field use. *Canad. Entom.* 85(6): 227-230.

Monro, H. A. U. 1935. The ecology of the pine sawfly (*Diprion simile* Htg.). Unpublished thesis, McGill University.

Morris, R. F. 1949. Frass-drop measurement in studies of the European spruce sawfly. *Univ. of Mich. School of For. and Cons. Bulletin No. 12.*

Rhumbler, L. 1929. Zur Begiftung des Kiefernspanners (*Bupalus piniarius* L.) in der Oberforsterei Hersfeld-Ost. 1926. *Z. angew. Ent.* 15: 137-158.

Schwerdtfeger, F. 1930. Beobachtungen und Untersuchungen zur Biologie und Bekämpfung des Kiefernspanners während des Frassjahres 1929 in der Letzlinger Heide. *Z. Forst-u. Jagdw.* 62: 65-93.

———————— 1931. Die Ermittlung der Mortalitat von Raupen während einer Insektenepidemic. *Anz. Schadlingsk.* 12: 85-90.

(Received August 25, 1955)

Synonymy of *Nomada fowleri* Cockerell with *N. obscurella* Fowler (Hymenoptera: Nomadidae)

By E. G. Linsley and J. W. MacSwain
University of California, Berkeley

Nomada obscurella Fowler, 1902, was originally described from one male from Berkeley, California, March 18, from *Ranunculus californicus*, under the name *N. obscura* Fowler, 1899 (preoccupied). *Nomada fowleri* Cockerell, 1903, was described from a female from Corvallis, Oregon, April 15, 1897 (A. B. Cordley). In connection with a study of some interrelationships of some *Ranunculus* bees we have become convinced that the two are synonymous. Although in general we disapprove of the association of sexes by elimination, in this case we regard the circumstantial evidence so strong as to leave little doubt that they represent the two sexes of a strikingly sexually dimorphic species. This evidence may be summarized briefly as follows:

Our studies of *Ranunculus* bees, their parasites and competitors have indicated a remarkable similarity between the components of this community at Corvallis, Oregon and its counterpart at Berkeley, California. Furthermore, these two forms occur at the same time in the season and are represented together in collections from various parts of the California Coast Ranges. In these collections there are no unassociated sexes of *Nomada* that could be regarded as the opposite sex of either *fowleri* or *obscurella*. In addition their numbers are approximately equal in our samples. Both forms exhibit an unusually wide range in size of from 5.0 mm. to 8.0 mm. in the males and from 5.0 mm. to 8.5 mm. in the females, with certain populations made up entirely of large individuals, others entirely of small individuals. Further, both forms differ markedly from the other species of *Nomada* associated with *Ranunculus* bees in that they spend relatively little time about the flowers. The females search the nesting areas of their host Andrenae and the males apparently seek them there rather than at flowers.

In 1954 we attempted the elimination (by capture) of a population of several thousand bees associated with a single field of *Ranunculus californicus*. This study confirmed earlier observations that in this community there were no Nomadae with sexes unassociated other than *N. fowleri* and *N. obscurella*. On this basis we propose this new synonymy.

We have reared this species of *Nomada* from the cells of *Andrena complexa* Viereck.

Temperature Relations of Ant-Lion Larvae (Neuroptera: Myrmeleontidae)[1]

By G. W. GREEN
Forest Insect Laboratory, Sault Ste. Marie, Ontario

INTRODUCTION

The common North American ant-lion, *Myrmeleon immaculatus* DeGeer, is generally distributed throughout the United States and has extended its range northward into Canada at various places. Throughout its range, the regular, cone-like pits of larvae of this species may be found in dry, sandy stretches that in an ecological sense constitute small, isolated desert regions.

Temperature is one of the most important of the physical factors with which desert species must contend. It is the purpose of this paper to present the results of an investigation of the effects of temperature upon the behaviour and activity of larvae of *M. immaculatus* in their natural habitat.

MATERIALS AND METHODS

This work was carried out at a summer field station operated by the Forest Biology Division at Pointe aux Pins, near Sault Ste. Marie, Ontario during the summer of 1950. Ant-lion larvae were collected from a sandy area near the field station and were liberated on and about a one-meter square plot (Fig. 1) that received the direct rays of the sun throughout most of the day. The boundary of the plot was outlined with a fine, white-painted copper wire suspended about 15 cm. above the ground and stretched around four posts driven into the ground at the corners of the plot. Red rings were painted on this wire at 10 cm. intervals as reference points to facilitate quick and accurate location of pits within the plot. The ant-lion population on the plot varied considerably during the summer with some of the larvae moving out of its bounds during peregrinations and others from surrounding areas moving in. Whenever the number of larvae on the plot dropped below 20, the population was supplemented by insects brought from the original collecting site.

Activity Observations

Observations of ant-lion activity were made every hour on the half-hour during test days. The time of observation, position of the pit within the plot, position of the larva within the pit, state of activity of the larva, and the number and kind of prey noted upon the plot were recorded. In addition, the position of each pit upon the plot was recorded at 0800 and 2000 hr. each day, and drying patterns and shadow patterns upon the plot were charted at intervals during the summer. These routine records were augmented by detailed notes on points of particular interest. Although most of the observations were made during diurnal periods, some observations were made during especially interesting nights.

Meteorological Equipment and Observations

Records from standard Stevenson screen instruments were obtained throughout the summer. Hourly records of wind speed and direction, type and amount of cloud, and type of precipitation were recorded between 0800 and 2000 hr. each day. These records were supplemented by spot readings made during days of particular interest and during those nocturnal periods when activity observations were made.

[1]Contribution No. 219, Forest Biology Division, Science Service, Department of Agriculture, Ottawa, Canada; based on part of a thesis submitted to the Department of Zoology, University of Toronto, in partial fulfilment of the requirements for the M.A. degree, 1953.

Habitat temperatures were measured with No. 24 and No. 30 copper-constantan thermocouples recording on a Brown Multiple Point Strip Chart Electronik Potentiometer. The use of this apparatus has been described in detail by Wellington (1950). Solar radiation measurements were made with an Eppley pyrheliometer, mounted on top of a 45-foot mast and recording on a Brown Single Point Potentiometer as described by Wellington (1950). A General Electric radiation meter was used in an attempt to measure solar radiation intensities incident upon the slopes of ant-lion pits but this instrument gave inaccurate readings when it was tipped out of its normal plane and records obtained with it had to be discarded.

The angle of incidence of the sun's rays on a horizontal surface was frequently measured at hourly intervals throughout the summer. The length of the shadow cast on a horizontal surface by a vertically-mounted wire mast of known height was measured and the angle of incidence of the sun's rays was calculated.

The compass position of the sun in the sky was obtained with an army marching compass. This compass was also used to lay out the activity plot and to orientate the instrument used in measuring the dimensions of ant-lion pits.

Ant-lion pits were measured with a simply constructed instrument. A wire mast with a wooden pointer was mounted so that it slid freely through a hole in the base of the apparatus. To measure the dimensions of a pit, the instrument was centred with the wire shaft directly above the pit base, and with the longitudinal axis of the apparatus orientated in a north-south direction. The instrument was then lowered gently until the base rested upon the sand at the pit's edge. The wire shaft was lowered to the pit base and the depth of the pit was read directly from a vertically-mounted scale behind the pointer. The north and south radii of the pit were read from scales inscribed in the transparent base of the instrument. The instrument was then rotated through 90° and the east and west radii were measured. These dimensions were used to calculate the slopes of the sides of the pit.

Detailed accounts of thermocouple arrangements used to obtain various temperature measurements are included in appropriate places through the text. All times quoted are Eastern Standard.

RESULTS

Temperature Measurements of the Sand and the Air Close to the Sand Surface

A site was chosen on the plot in which thermocouples were arranged to measure sand temperatures at the surface and at depths of 10, 20 and 40 mm. In addition, a series of thermocouples was mounted to measure air temperatures at heights of 5, 20, 100, and 500 mm. above the sand surface. Air temperature thermocouples were covered with small aluminum foil radiation shields of the type described by Wellington (1950). The site chosen for these temperature measurements received the direct rays of the sun from about 0930 hr. onwards. A light, flecked shadow fell over the area for a few moments at 1100 hr., and a heavy shadow caused by the meteorological tower passed through the area between 1400 and 1530 hr. At all other times between 0930 and 1830 hr. the area was in direct sunlight.

Data for two days, July 28 and July 31, have been selected from the records for graphic representation of temperature variations on clear and cloudy days respectively. Figure 2A illustrates differences in the daily march of sand temperatures at various depths during these two days. The most obvious difference in these two figures is the range of diurnal temperature fluctuations. During the

clear day, this range extended from about 18 to 51°C., a maximum variation of about 33°. In contrast, during the cloudy day, the maximum temperature variation was in the neighbourhood of only 8°. These two figures also demonstrate the great differences that exist between the temperatures of the sand at

Fig. 1. Observation plot for studies of the activity of larvae of *M. immaculatus*. Some of the thermojunctions are shown in position measuring sand and air temperatures. Photograph by W. G. Wellington.

various depths on clear days and the relatively small differences between the same measurements on overcast days.

Since sand temperatures fluctuate most on clear days, the temperature curves shown in Fig. 2A for such a day are considered in more detail below. The heavy, solid line in Fig. 2A represents the temperature curve at the sand surface. Accurate surface temperature measurements are extremely hard to obtain, for the rapid temperature changes that occur at very short distances both above and below the soil surface make it essential that the sensing element of the recording apparatus be set and maintained in a very critical position. This is especially so during the hotter parts of the day, when violent eddy diffusions occur in the boundary layer. The temperature curve for the surface sand appears normal between 0800 and 1000 hr., and from 1530 hr. on, but does not appear valid between these two periods. The thermocouple at the sand surface was probably displaced sufficiently to cause this anomaly during the hotter parts of the day. Had the thermocouple been exactly in place, the temperature curve for the surface sand would have risen above all other points measured. The other curves are good examples of the normal daily march of temperatures within a sand mass during a day characterized by high insolation levels. In the earlier parts of the day, when all temperatures are increasing, the rate of temperature rise and the maximum temperatures attained decrease with depth in the sand. This is due to the lag imposed by the thermal conductivity of the sand mass. At approximately 1400 hr., a heavy shadow caused by the meteorological tower passed over the plot, with the result that the temperature of the sand at most depths began to decline. The temperature of the sand at the 40 mm. level continued to rise slowly during this period, again due to the thermal conductivity of the sand mass. In general, the rate of cooling of the sand and the range of daily temperature fluctuations decrease with depth. This is characteristic and is of some importance when one considers forms that live in the upper parts of the soil. The complete reversal that occurs in all the temperatures shown in Fig. 2A between 1500-1600 hr. is again characteristic. The temperature of the sand is now seen to increase with depth. This inversion in sand temperatures occurs even while some insolation is incident upon the soil surface. It may be explained on the basis of the incoming radiation, on the wane, at this hour, not being sufficient to counteract the loss of heat from the ground to the atmosphere through long wave outgoing radiation and convection.

Differences in sand temperature with depth are considerable on the clear day, approximately 8°C. between 10 and 40 mm. at 1300 hr., and 5°C. at 2130 hr. Temperature variations of this degree could be very important to an insect inhabiting the area, especially if they occur when temperatures within the habitat are approaching levels lethal for the insect.

Figure 2B shows the daily march of air temperatures at different heights above the sand surface on the two days. Again, temperature fluctuations are more extreme on clear than on cloudy days. Although no air temperature inversion is shown during the early nocturnal period, it does occur on still, clear nights characterized by excessive back radiation from the ground. The general shapes of the air temperature curves are seen to correspond quite closely to those of the sand and illustrate the great effect that soil temperatures have upon the layer of air close to the earth's surface.

Radiation intensities, as measured with the pyrheliometer, are illustrated in Fig. 2C. The exposure of this instrument differed from that of the temperature measurement site, both in elevation and in the fact that it was exposed to the

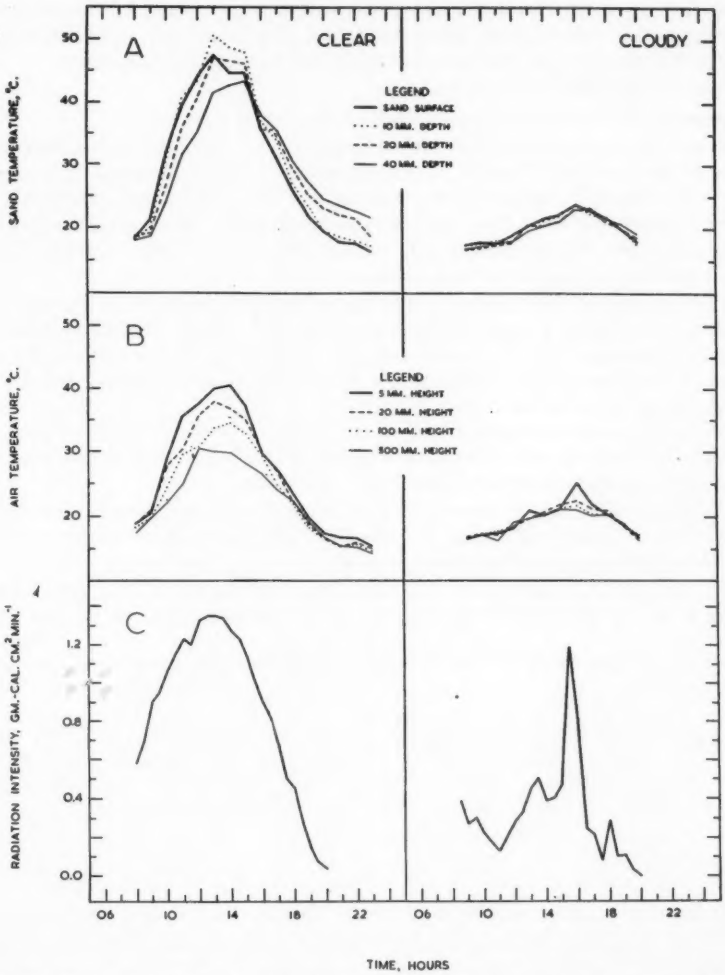


Fig. 2. Comparison of sand temperatures (A) at different depths, air temperatures (B) at different heights, and solar radiation values (C) on a clear and a cloudy day in July.

direct rays of the sun throughout the day. Therefore, the shadow patterns affecting sand temperatures are not evident in the radiation traces. The curves are shown here to demonstrate the normal diurnal march of incoming short-wave radiation during the two days. The dependence of sand temperature on solar radiation is quite evident.

Temperature Relations Within Pits of Ant-Lion Larvae

In the foregoing section, variations in temperature between different parts of the gross habitat of ant-lion larvae have been described. It has been shown that the diurnal march of temperatures fluctuates widely, and that temperature levels reached by various parts of the gross habitat may be quite extreme. Since

the ant-lion larva has become adapted for life in such a habitat, it is of interest to examine the temperature relations within the larval pit in an attempt to discover whether the pit aids in moderating the temperature conditions to which the animal might otherwise be exposed.

Temperature measurements of the sand in the surface layers

A test pit was constructed with a depth of 27 mm. and a diameter at the surface of the sand of 68 mm. These dimensions, which resulted in a slope of 38.5° to the pit sides, are about average for ant-lion pits in the area at this time of year (Green, 1953). This test pit was constructed in an area that received the direct rays of the sun throughout the day, except between 1100 and 1200 hr. when it was in the shadow of a red pine tree.

Thermocouples for surface temperature measurements were situated halfway down the N, S, E, and W slopes of the pit. Other thermocouples were arranged to measure the temperature of the surface sand at the pit's edge and of the sand 1 mm. below the pit base in the position normally occupied by the head and mandibles of an ant-lion larva.

The sun's compass position was obtained every hour on the half-hour, and the angle of incidence of its rays on the flat surface sand was measured at the same time with the instrument previously described.

The data collected for August 12 have been chosen for presentation because this day was relatively clear, and the effects of insolation on the temperatures of the sand in the various sites are then greatest.

The angles of incidence of the sun's rays on the horizontal sand surface, the slope of the pit directly facing the sun, and the slope of the pit facing

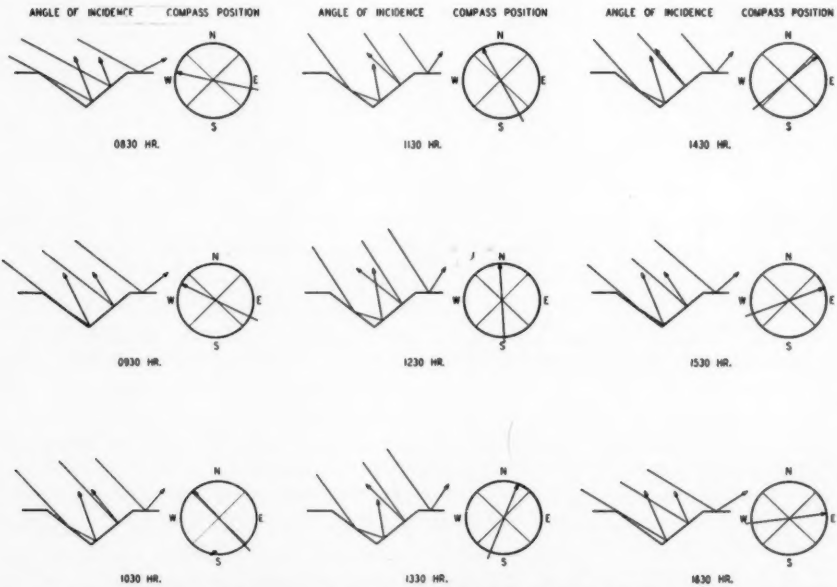


Fig. 3. Angles of incidence and angles of reflection of the sun's rays on the horizontal sand, on the slope of the pit directly facing the sun, and on the slope of the pit facing directly away from the sun at hourly intervals between 0830 and 1630 hr. August 12, 1950. Compass positions of the sun in the sky and the sector of the pit receiving the sun's direct rays are indicated by the arrows within the circles.

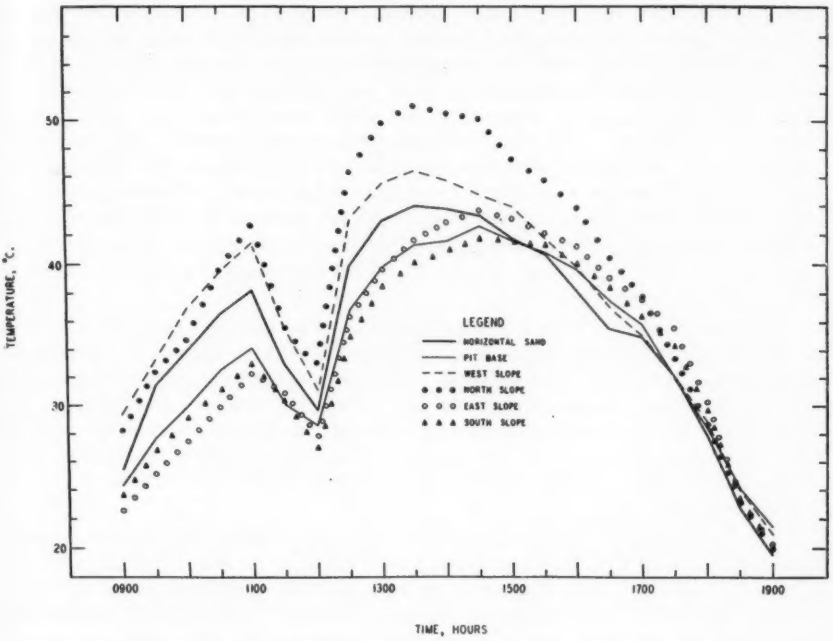


Fig. 4. Comparison of sand surface temperatures in and about an ant-lion pit during a relatively clear day in August.

directly away from the sun were calculated from the data. Fig. 3 shows the angles of incidence of the sun's rays on these surfaces at different times of the day. This figure also shows the angles of reflection of the sun's rays from the pit slopes assuming that these act as perfect, flat reflectors.

Until approximately 0930 hr. the pit slope facing away from the sun is in shadow. From 0930 hr. until sometime between 1530 and 1630 the slope of the pit facing away from the sun receives its direct rays at low angles of incidence. During this period, these rays are reflected and augment the already high insolation received by the slope of the pit facing the sun. Thus, maximal heating per unit of incident solar radiation should occur on the horizontal sand at solar noon, and on the pit slope facing the sun during the period two hours on either side of solar noon.

The sun's compass position in the sky is such that the W sector of the pit (the sector between NW and SW) is facing the sun until approximately 1030 hr., when the N sector of the pit begins to face the sun more directly. This sector receives the most direct rays of the sun until approximately 1430 hr., when the more direct rays move into the E sector of the pit.

Fig. 4 shows temperature curves for the sand on the horizontal surface at the pit's edge, on the surface of the slopes of the pit facing in the four cardinal compass directions, and of the sand 1 mm. below the pit base. Until approximately 1030 hr., the surface sand on the W slope remains at a higher temperature than any other point measured. At this time the temperature of the sand on the N slope rises above all others measured. These phenomena are exactly as would

be expected on the basis of the sun's position charts (Fig. 3) during this period. The more direct rays of the sun become incident on the E slope of the pit at approximately 1430 hr. but the temperature crossover between E and N does not occur until 1700 hr., because by 1430 hr., although the angle of incidence of the sun's rays on the E slope of the pit is still near the normal, their heating powers are declining. The effect of these rays on the E slope of the pit, therefore, is to slow the normal temperature decline of this slope at this time of day. The N slope of the pit was heated by direct and reflected radiation to approximately 10°C. above the E slope during the hotter parts of the day, and with the normal temperature decline during the afternoon, it takes some time for the N slope sand to cool below that of the E. The temperature crossover, when it does occur, is at best very weak.

The temperature of the horizontal sand remains between that of the hotter W and N slopes and the cooler E and S slopes until late afternoon when all of the temperatures begin to converge. The temperature of the pit-base sand remains consistently below that of the surface sand at the pit's edge and the pit slopes facing the sun until temperatures converge later in the afternoon. Maximum depression (4.5°C.) of the pit-base temperature below horizontal sand surface temperature occurs during the morning hours and lessens gradually from 1330 hr. on.

The possession of a pit has therefore markedly altered the surface temperature conditions to which an ant-lion would otherwise be exposed.Until approximately 1530 hr. on a clear summer's day, the pit-base temperature remains from 3 to 5°C. below the temperature of the surface sand. The surface temperatures of the sand on the pit slopes facing the sun remains from 0 to 10°C. above the temperature of the pit-base sand while the pit slopes facing away from the sun closely approximate the temperature of the pit base throughout most of the day.

Temperature measurements of the sand below the surface

On clear days it was observed that, as the temperature of the sand at the pit base rose to high levels, ant-lion larvae moved back through the sand from their normal feeding positions and rested between the pit base and the circumference of the pit. It was assumed that larvae were moving to cooler sites. Consequently, temperature measurements were made of the sand at pit-base level, but at distances of 15 and 34 mm. from the pit base along the four cardinal compass lines.

Table I presents mean temperature differences between the sand at the pit base and that in the N, S, E, and W sectors of the pit at distances of 15 and 34 mm. from the pit base. During the morning, the temperature of the sand in all sectors remains below that of the sand at the pit base. The sand in the S and E sectors is coolest during this period and that in the N and W sectors warmest. This point is further brought out in Fig. 5, where the temperature curves for the pit base and the warmest and coolest sectors of the pit at the 15 mm. level are compared. During the afternoon, the situation is somewhat different, with the S and W sectors of the pit being the coolest, and the N and E sectors the warmest. Temperature differences are not as great as in the morning and some of the sectors contain sand that is warmer than that at the pit base. These points are brought out in Fig. 6, which is the afternoon counterpart of Fig. 5.

It will be appreciated that temperature differences measured in these sites are substantial, and that they could conceivably exert some influence on the distribution of larvae within their pits as the day goes on.

TABLE I

Comparison of differences in the temperatures of the sand at pit-base level but removed from the pit-base by 15 and 34 mm. along the four cardinal compass lines during the morning and afternoon periods of a relatively clear day. Temperature differences quoted are the mean differences from the temperature of the sand at the pit-base.

15 mm. from the pit-base								
Period	0900–1300 hr.				1300–1900 hr.			
Position	North	West	East	South	North	West	East	South
$\bar{x}$ diff. °C.	−0.73	−2.15	−2.92	−4.31	+0.33	−1.44	+0.80	−0.34
34 mm. from the pit base								
$\bar{x}$ diff. °C.	−4.84	−4.05	−5.23	−6.68	+0.10	−1.04	+0.22	−1.74

Positions Adopted by Ant-Lion Larvae Within Their Pits

In the foregoing sections, much emphasis has been placed upon the pit of the ant-lion larva and upon the temperature levels to which the sand at different points within the pit boundary may be raised. It has been shown that the possession of a pit provides the ant-lion larva with an environment that gives it, first, temperature conditions at the pit base that are, in general, several degrees

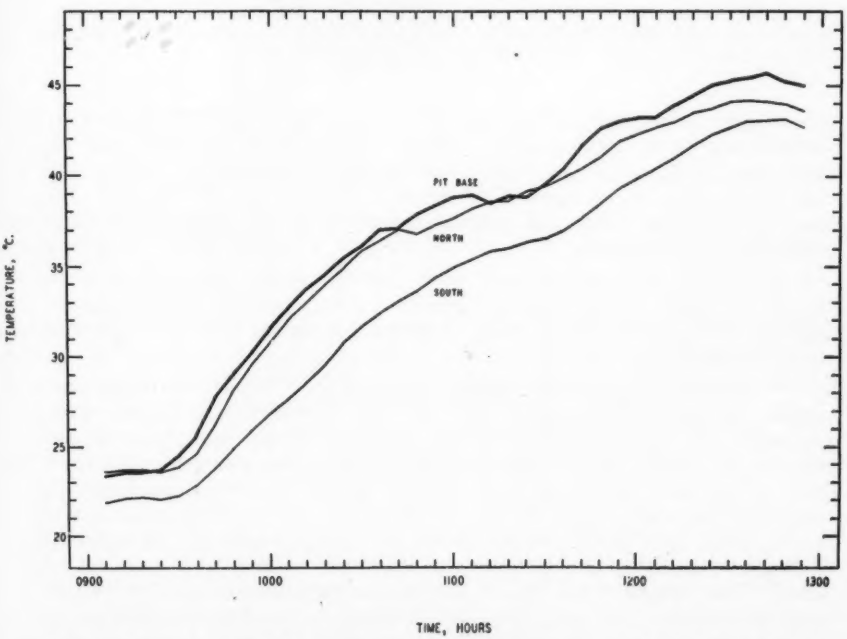


Fig. 5. Comparison of pit-base temperature and the temperature of the sand at the same level 15 mms. back from the pit base, in the *north* and *south* sectors of an ant-lion pit between 0900 and 1300 hr. on a relatively clear day.

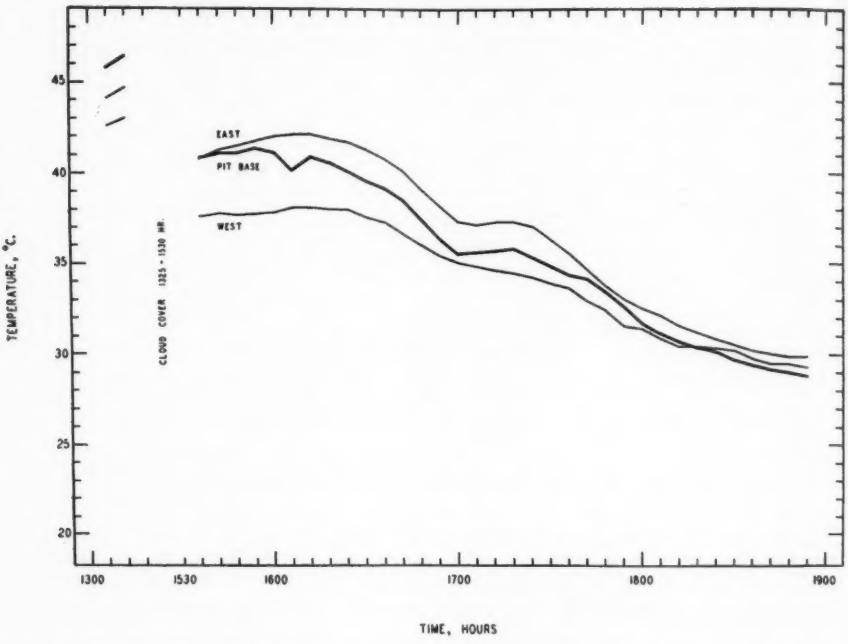


Fig. 6. Comparison of pit-base temperature and the temperature of the sand at the same level 15 mm. back from the pit base, in the *west* and *east* sectors of an ant-lion pit between 1300 and 1900 hr. on a relatively clear day.

below that of the horizontal surface sand on clear days, and second, temperature conditions at short distances back through the sand at the pit base that may be more than 10°C. below that of the sand in the surface layers. It is of interest then to examine the movements of larvae about their pits to discover whether they orientate themselves in a manner related to the range of temperature conditions found therein.

As activity observations were made throughout the summer, the sector of the pit occupied by the body of each larva was recorded. Movements of the larvae in relation to the temperature of the sand at the pit base were also observed at some length.

At pit-base temperatures ranging from 10 to 25°C., larvae adopt positions within their pits such that their heads and mandibles are lying for the most part exposed, or covered only by a thin layer of dust at the pit base. In such positions they are most effective in capturing prey that drop into their pits. Below 10°C., larvae move back into the sand at the pit base by distances depending, in part, on the degree to which the pit-base temperature is lowered. At pit-base temperatures as low as 5°C., a response to an ant dropped into the pit may still be obtained. Larvae move out from under the sand, capture the insect, and retreat with it into the sand mass again. At pit-base temperatures above 25°C., larvae move their heads back under the sand, but may leave their mandibles exposed. They retain this position until the temperature of the sand at the pit base rises above 35°C., at which time the larvae retreat into the sand into regions that have been shown (Table I) to be much cooler than the sand at the pit base. At

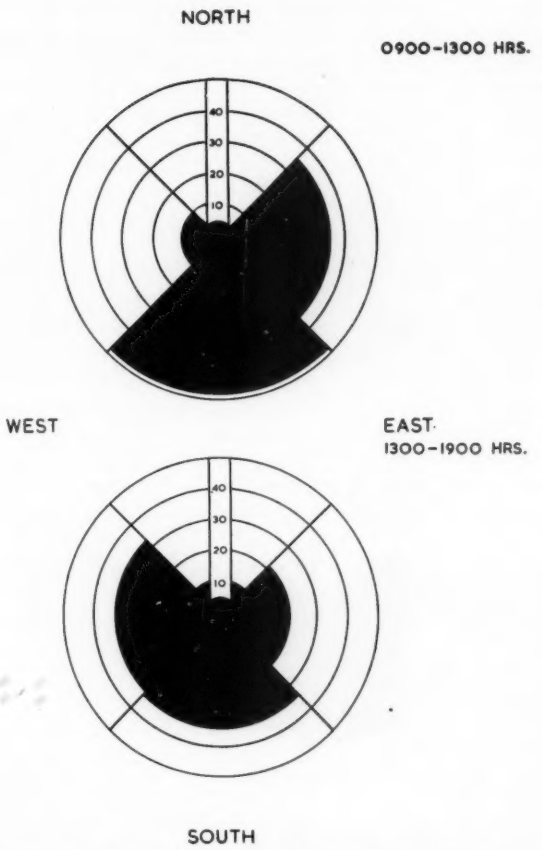


Fig. 7. Positions adopted by ant-lion larvae within their pits during the morning and afternoon periods of *relatively clear days* throughout the summer. The scale in this figure is per cent.

temperatures above 35°C., the larvae still respond to insects dropping into their pits by moving out to the pit base and then into the sand mass once more. Larvae seldom move to the pit base if the sand there is heated to 45°C., and were never observed to move out at pit-base temperatures in excess of 48°C.

In analysing the data collected on the sector of the pit occupied by the larva, the original records were somewhat simplified. For example, if an insect were recorded as lying in the SW sector of its pit, it was checked as being in the S and the W sectors. Hence, in the final analysis, the insects were recorded as lying in the N, S, E, or W sectors of the pits. In this form, the data were broken down into clear and overcast days, and these further broken into a morning period between 0900 and 1300 hr., and an afternoon period between 1300 and 1900 hr.

Fig. 7 presents results accumulated during clear days throughout the summer. During the morning there is a high concentration of larvae in the S and E pit sectors, with very few in the N and W sectors. In the afternoon, this distribution is markedly altered with most of the larvae now appearing in the S and the W

B & Z Library

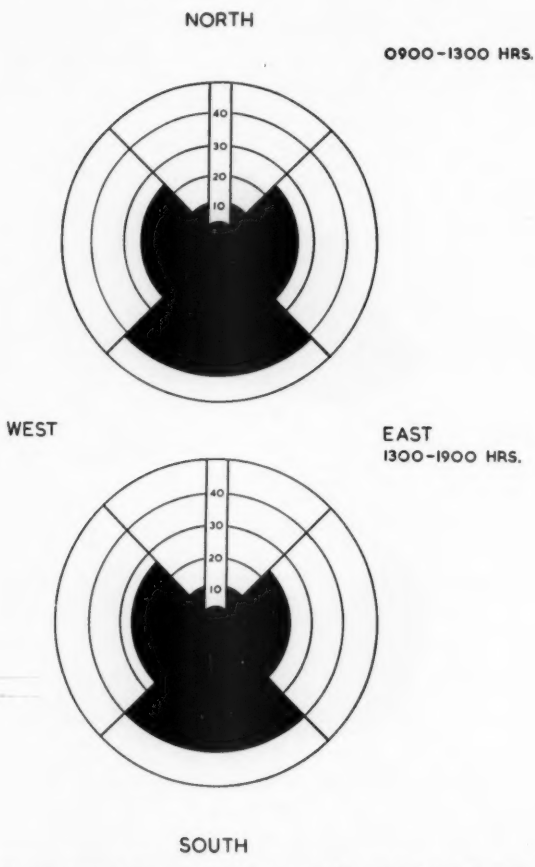


Fig. 8. Positions adopted by ant-lion larvae within their pits during the morning and afternoon periods of *overcast days* throughout the summer. The scale in this figure is per cent.

sectors of the pits. On clear days, then, ant-lion larvae orientate themselves so that their bodies remain in the coolest available sectors (Table I) of the pits.

Fig. 8 presents results accumulated for overcast days throughout the summer. Here most of the larvae lie in the S pit sector, few in the N, and an intermediate number in the E and W sectors. The distribution remains much the same throughout the day, without the definite shift seen on clear days. Such a distribution might well be expected since it has been shown (Fig. 2) that sand temperatures differ but slightly on overcast days and do not reach extreme levels. Larvae are not forced to move to cooler sites and the distribution therefore remains quite static.

The Effect of Pit-Base Temperature Upon the Feeding Activity of Larvae of *M. immaculatus*

During the summer of 1950, temperature and activity records were made periodically from early June until mid-August. In relating temperature of the sand to larval activity, measurements were made 1 mm. below the pit base. At

first, such measurements were made in a pit occupied by an ant-lion larva, but this procedure was abandoned because the larva reacted to the presence of the thermocouple, and either buried the sensing element or vacated the pit. For this reason, a test pit was constructed to the dimensions given earlier. This pit was so situated that its exposure was comparable to that of most of the active pits on the plot. During activity observations, only those naturally occurring pits with exposures comparable to that of the test pit were considered.

An ant-lion larva was classed as either active or inactive. A larva was considered active if its mandibles were exposed at the pit base, if it could be seen pit clearing, if it reacted to a few grains of sand rolled down the pit slope, or if it attempted to capture a living red ant, *Lasius niger neoniger* Emery, dropped into its pit. Otherwise, the larva was considered to be inactive. Activity observations of this type were made at hourly intervals on test days, temperature measurements at the pit base being recorded continuously. In all, 2,356 temperature-activity observations were made during the summer.

In the analysis of these data, a class interval of 3°C. was used, and the percentage of active larvae plotted against pit-base temperature. These results are shown in Fig. 9. The total number of activity observations is represented within each activity bar. Temperature levels at either end of the activity range were seldom experienced with the result that activity observations at these levels are few.

Fig. 9 shows that the activity of ant-lion larvae increases with temperature from a probable zero level near 2°C. to a point where approximately 70% of the larvae on the plot are active by the time that the temperature of the pit base

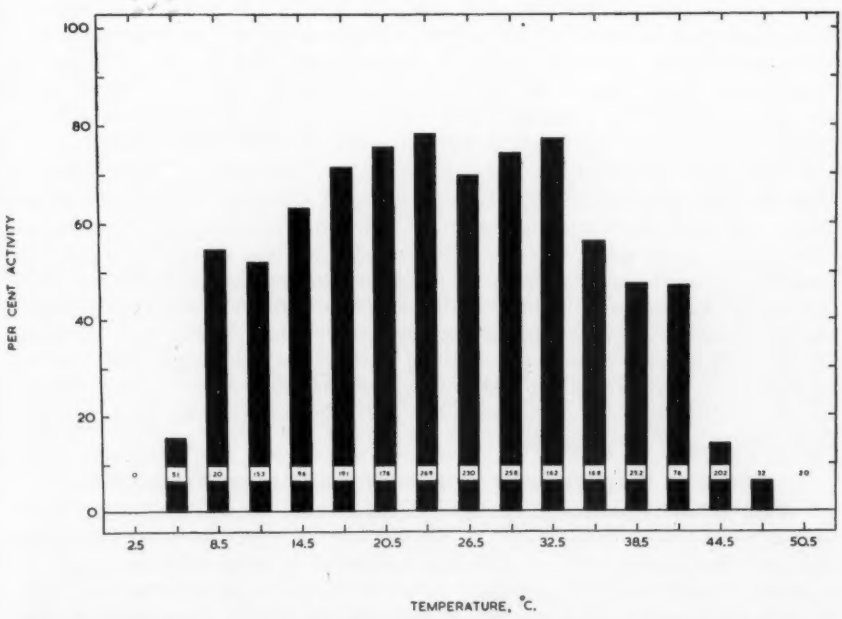


Fig. 9. Activity of larvae of *M. immaculatus* in relation to sand temperature at the pit base. Inserted figures are the number of observations at each temperature level.

has risen to 16°C. Activity proceeds at high levels between 16 and 34°C., with never less than 70% of the larvae on the plot active throughout this range. When the temperature exceeds 34°C., the number of active larvae begins to decline and reaches zero at about 48°C. Thus, larvae remain active through a temperature range of some 46°.

It might be well to mention here that although occasionally 100% of the larvae on the plot may be active this seldom occurs, so that the averages of grouped data, as in Fig. 9, will always remain below 100%. This type of inactivity at favourable temperatures has been termed *asitosis* by Wheeler (1930) and must not be confused with the inactivity caused by temperatures beyond the temperature-activity range.

To demonstrate the activity patterns that may be expected on clear and on cloudy days throughout the summer months, the results of two typical days have been selected from the data. In each case, observations were made at two-hour intervals during the nocturnal period and at one-hour intervals during the day. Temperature measurements at the pit base were again recorded continuously.

Fig. 10 shows the activity patterns of the larvae on the plot and the temperature curves for the sand at the pit base during the two type days. The data for August 11 and 12 are representative of activity during clear periods. The night of August 11 and the early morning of August 12 were clear and windless. Throughout this period, outgoing radiation from the ground cooled the sand at the pit base to approximately 4°C. by 0500 hr. Larval activity followed the temperature decline until, by 0630 hr., only 6% of the larvae on the plot were active. August 12 was relatively clear. Small patches of cirriform cloud began to form by 1400 hr., but never developed to more than two-tenths coverage and had no significant effect on solar heating. Larval activity followed the temperature rise until 1130 hr. when, corresponding to a pit base temperature of approximately 35°C., it began to drop off once more. By 1230 hr. the temperature of the sand at the pit base exceeded 45°C., and all of the larvae on the plot were inactive. A period of complete inactivity prevailed until 1530 hr., when larvae became active again with declining pit-base temperatures.

The night of August 7 began partly cloudy and calm. Skies cleared by 2000 hr. and remained so until 0500 hr. the next morning. From 0500 hr. on, cirrus and cirro-cumulus cloud began to build up, thickening to altostratus and completely covering the sky by 1000 hr. During the nocturnal period, the temperature of the sand at the pit base never dropped below 11°C., and larval activity proceeded at a high level throughout the night with only a shallow decline coinciding with minimum pit-base temperatures in the early morning. As the sand warmed later in the morning, activity increased again and remained at high levels throughout the rest of the day with no cessation about mid-day as was usually the case on warm, clear days characterized by high insolation and extreme sand temperatures.

Activity of Prey Species in Relation to Sand-Surface Temperatures

Park (1941) has stressed the continuous activity that prevails within most animal communities throughout the diurnal and nocturnal periods. He points out that there seems to be a maximum utilization of space and time, and that while one species may be inactivated by a certain level of a set of environmental factors, another becomes active at that time. In the previous section, it has been demonstrated that the temperature-activity range of larvae of *M. immaculatus*

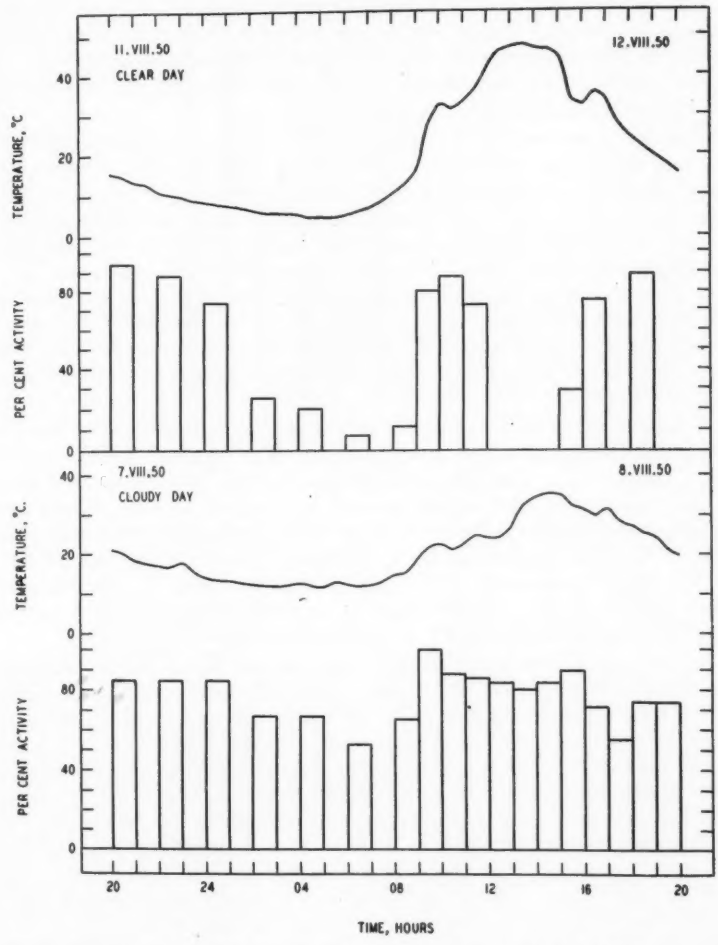


Fig. 10. Comparison of the activity of larvae of *M. immaculatus* and the temperature of the sand at the pit base on a clear and an overcast day in August.

extends through a very broad range of temperatures and that the larvae are active throughout the night as well as during the day, providing temperatures do not become extreme. It is now of interest to examine the temperature-activity ranges of some of the more important prey of ant-lion larvae in the Sault Ste. Marie district and to compare these ranges with that found for ant-lions.

Two species of ants, *Lasius niger neoniger* (Emery) and *Formica fusca* L., were present in such large numbers in the experimental area that they formed the bulk of the diet of ant-lion larvae on the plot. The reactions of these two species to sand-surface temperatures were studied. In the case of *Lasius*, a thermocouple was arranged to measure the surface temperature of the sand at the entrance to one of their nests. Observations were made of the number of ants leaving the nest during five-minute periods on type days. The activity of

Formica was determined by counts made of the number of ants moving through a one-meter square plot during five-minute observation periods. Temperatures for relation to these observations were measured at the sand surface in the centre of the plot. Both of the sites chosen for these measurements received the direct rays of the sun throughout most of the day.

Temperature and activity observations of the type described above were made during three days for *Formica* and during four days for *Lasius*. In the analysis of these data, a class interval of 3°C. was used. The mean numbers of insects of both species active at different temperature levels are plotted in Fig. 11, where their temperature-activity ranges are compared with the temperature-activity range previously shown (Fig. 9) for larvae of *M. immaculatus*. The numbers of observations made of ant activity at the various temperature levels are indicated within the activity bars in Fig. 11. The number of observations of ant activity at any temperature level was low, but the resulting activity patterns illustrate the difference in the temperature ranges of activity of *L. n. neoniger* and *F. fusca*.

F. fusca was never observed on the plot when the temperature of the surface sand dropped below 20°C. or rose above 49°C. Optimal activity occurred between 32 and 39°C. The full activity range for this species covered approximately 29°. Talbot (1946), working with the related species, *Formica pallidefulva schaufussi incerta* Emery, found it to be active above ground between 15.5 and 43°C., with optimal activity occurring between 29.4 and 35°C. Although the range of activity of *F. fusca* is slightly higher in the temperature scale than that of *F. p. s. incerta* there is no doubt that both are hot-weather species, exhibiting optimal activity at high temperatures.

It is unfortunate that lower temperatures did not occur during observations of the activity of *L. neoniger*. The lower end of the temperature scale presented in Fig. 11 falls far short of the expected lower activity level of this species. However, it is certain that the temperature-activity range of *L. n. neoniger* extends at least as low as 6°C., for small numbers of this species have been observed on the ant-lion plot at temperatures as low as this. Fig. 11 indicates that the activity of *Lasius* drops from an optimum at or below 14.5°C. to complete cessation of above-ground activity in the neighbourhood of 32.5°C. Talbot (1946), working with the same species, found the insect very active at between 10 and 15.6°. She found also that the activity dropped off with increasing temperatures until it stopped between 32 and 38°C.

Singly or together, *L. n. neoniger* and *F. fusca* constitute a food supply that may be expected to be present throughout most of the rather broad temperature-activity range of larvae of *M. immaculatus*. Both species are active during that part of *M. immaculatus*' activity range that falls between 20.5 and 30.5°C.; *F. fusca* being present above 30.5°C. and *L. n. neoniger* below 20.5°C.

DISCUSSION

Animals exploiting xeric habitats such as dry sandy stretches must contend with extreme fluctuations in soil surface temperatures. Such sites are low in nutrients and support only a sparse growth of xerophytic plants. The absence of dense ground-cover permits the ready penetration of the sun's rays to the soil surface by day and unobstructed back radiation to the atmosphere by night with attendant high diurnal and low nocturnal surface temperatures. Animals living in this type of habitat may be expected to possess inherent anatomical and physiological adaptations that allow them to tolerate temperatures too extreme for most other forms of life. In almost all cases, these adaptations are augmented

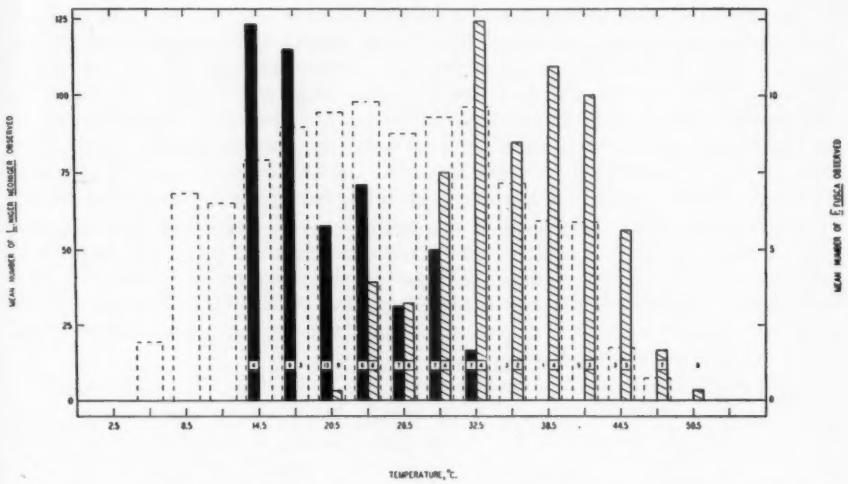


Fig. 11. Comparison of the temperature-activity ranges of *L. niger neoniger* (solid bars), *F. fusca* (cross-hatched bars), and *M. immaculatus* (clear bars). The number of observations at each temperature level is indicated in a small square within each activity bar.

by behaviouristic peculiarities that help to modify the range of temperature conditions to which the animal is directly exposed.

According to Wheeler (1930) the genus *Myrmeleon* represents the culminating stage of at least four different phylogenetic stages of behaviouristic development within the family Myrmeleontidae. These run from a free, active, predatory stage with little attempt at concealment, through more lethargic forms that bury themselves in the sand and detritus, to those that make pitfalls but retain the ambigradient gait of the former stages, and finally to *Myrmeleon*, which has become more sedentary and completely retrogradient. It has been shown in this study that the temperature of the sand 20 mm. below the surface may be as much as 8°C. below that of the surface sand. This presents a sharp temperature gradient that may be used to advantage by predacious forms, except that by simple burrowing to lower and consequently cooler levels they cannot effectively capture prey. By virtue of its pit-forming behaviour, the larva of *M. immaculatus* has taken advantage of this vertical temperature gradient while retaining a very effective predatory mode of life.

The pit of this species, while serving as an admirable trap for prey, removes the ant-lion larva from the hot surface sand. The structure of the pit provides the larva with temperature gradients that it utilizes as the day progresses. Possession of a pitfall permits larvae to remain active through a period in which the surface temperatures would be too extreme for activity were they exposed to it. In terms of horizontal sand-surface temperatures that range as much as 10°C. above the temperature of the sand within the coolest sector of the pit during the hotter parts of the day, larvae of *M. immaculatus* may remain functional through sand surface temperatures as high as 52°C. (126°F.). Thus the protection afforded by the pitfall allows ant-lion larvae to operate at surface temperatures between 2 and 52°C., a range that more than includes the temperature-activity ranges of most of their insect prey.

Larvae of *M. immaculatus* are not usually found in areas as open and exposed as that used during this study, and indeed, the sites that they seem to select are usually partly shaded by vegetation, detritus, or man-made structures. An open site was chosen for this study so that a greater range of temperature might be investigated than would otherwise be offered. The fact that larvae thrived in such a site throughout the summer indicates that they are well able to cope with extremes in temperature if they are forced to. Movement to, and the selection of, partly shaded sites is but another behaviour characteristic of adaptive value.

The resistance of the animal to desiccation may be enhanced by its underground mode of life. Certainly, air movements over its body are kept to a minimum with a corresponding decrease in the evaporative power of the surrounding air, and it is not impossible that a shell of relatively moist air is built up around the larva through evaporation from the body and kept from escaping to the outside by the sand mass.

Although larvae of *M. immaculatus* in the Sault Ste. Marie district never appear to lack a plentiful supply of prey, except during the hot noon day periods, they are well adapted should such a shortage occur. Larvae have been maintained in the laboratory for periods of up to two months without feeding. In the field they often go into short periods of asitosis, during which no food is consumed.

SUMMARY

1. The relations between sand temperature and depth, and air temperature and height, as they exist in exposed sandy stretches in the Sault Ste. Marie district are demonstrated. It is shown that sand temperatures decrease with depth and air temperatures with height during periods of strong or increasing radiant heating. These temperature relations are reversed when the rate of radiant cooling exceeds that of radiant heating. Solar radiation is an extremely important factor governing sand temperatures.

2. Surface temperature relations of the sand at various points within the pits of larvae of *M. immaculatus* are given. During clear days, the temperature of the sand at the base of the pit remains up to 5°C. below that of the surface sand at the pit's edge. Temperatures of the surface sand on the N and W slopes remain much higher than the temperature at the pit base during the entire day, while surface temperatures of the S and E slopes remain from slightly below to slightly above pit-base temperatures during this period. Surface temperatures on the hottest slopes may exceed pit-base temperatures by as much as 10°C. during the hotter parts of clear days. During overcast days, temperature differences are much smaller.

3. Temperature relations of the sand below the surface within pits of larvae of *M. immaculatus* have been investigated. During clear days, by moving within a radius of 34 mm. from the pit base at pit-base level, larvae may encounter regions that range from 0.73 to 6.68°C. below the temperature of the sand at the pit base during the morning and from 0.80 above to 1.79°C. below it during the afternoon. The coolest sectors of the pit are the S and E sectors in the morning, and the S and W sectors in the afternoon. During overcast days, temperature differences within pits are much smaller than on clear days.

4. During clear, warm summer days, larvae of *M. immaculatus* orientate themselves within their pits so that their bodies are in the coolest regions available to them. During the mornings, the majority of the larvae are found in the S and the E pit sectors, and in the afternoon, in the S and W sectors. During overcast days, the orientation is not so definite.

5. Larvae of *M. immaculatus* remain active through temperatures of the sand at the pit base ranging from approximately 2 to 48°C. Larvae may be inactivated by high noon-day temperatures or very cold temperatures at night.

6. The above-ground activity of two species of ants, *L. niger neoniger* and *F. fusca*, two of the most important of the prey species of *M. immaculatus* larvae, have been investigated in relation to sand surface temperature. *L. n. neoniger* is active at temperatures between a probable low of 4°C. and a high of 35°C. Temperatures permitting, it is active by day and by night. *F. fusca* becomes active above ground at surface temperatures of about 20°C. and ceases its above-ground activity as temperatures exceed 50°C. This species is not active at night. Singly or together, these two ant species constitute a food supply that is present throughout most of the temperature-activity range of larvae of *M. immaculaus*.

ACKNOWLEDGMENTS

The investigations upon which this paper is based, were carried out in addition to the author's regular duties while employed by the Department of Agriculture, Forest Biology Division. I am grateful to this organization and to M. L. Prebble, then Officer-in-Charge of the Forest Insect Laboratory, Sault Ste. Marie, Ontario, for permission to use the meteorological installations at the station during this work. I am also indebted to W. G. Wellington, Head, Bioclimatology Section, Forest Biology Division for his guidance in the planning of this project and for his suggestions and criticisms as the work progressed.

This paper is based on part of a thesis submitted to the Department of Zoology, University of Toronto, Toronto, in partial fulfilment of the requirements for the M.A. degree, 1953. I am grateful to J. R. Dymond, C. E. Atwood, and others of the Department of Zoology for suggestions and criticisms during the analysis of the data and the preparation of the original manuscript.

REFERENCES

Green, G. W. 1953. The effects of physical factors upon the behaviour and activity of larvae of the common North American ant-lion with notes on its morphological and physiological adaptations to life in a xeric habitat. M.A. thesis, Department of Zoology, University of Toronto, Toronto, Canada.

Park, O. 1941. Concerning community symmetry. *Ecology* 22: 164-165.

Talbot, M. 1946. Daily fluctuations in the above-ground activity of three species of ants. *Ecology*, 27(1): 65-70.

Wellington, W. G. 1950. Effects of radiation on the temperatures of insectan habitats. *Sci. Agr.* 30(5): 209-234.

Wheeler, W. M. 1930. Demons of the dust. W. W. Norton and Co. Inc. Publishers, New York.

James Malcolm Swaine
1878-1955

Dr. J. M. Swaine, former Director of Science Service, Canada Department of Agriculture, died at his home, 484 Brierwood Avenue, Ottawa, on November eleventh, shortly after his seventy-seventh birthday.

Dr. Swaine was born at Barrington, Nova Scotia, the son of Capt. James Swaine and Sophia Hamilton. He attended school at Yarmouth, Nova Scotia and later the Provincial Normal School at Truro. Subsequently he taught school at South Ohio, Nova Scotia, and later entered the Nova Scotia Agricultural College. In 1905 he graduated from Cornell University with his B.S.A., to be followed by his Master's.

For two years Dr. Swaine was Assistant in Entomology and Zoology at Cornell. He returned to Canada in 1907 and for the next five years lectured in the same subjects at Macdonald College of McGill University. In 1912, having attained international fame for his research on forest entomology, he was brought to Ottawa to become Officer-in-Charge of the Forest Insect Section of the Division of Entomology. On presentation of his thesis on Canadian Bark Beetles he was awarded his Ph.D. by Cornell University. In 1923 he was appointed Associate Dominion Entomologist.

Dr. Swaine was regarded throughout his lifetime as a scientist of high standing and ability. He was the author of many papers on entomology and other scientific subjects and was honored by being made a member of the Royal Society of Canada.

During the Second World War Dr. Swaine served on the Agriculture Supply Board. For his services he was decorated with the Order of a Companion of the British Empire.

He was a member of the American Association of Applied Science, the Entomological Society of America, the Entomological Society of Ontario, the American Association of Economic Entomologists, and the Quebec Society for the Protection of Plants.

He was a Fellow of the Royal Society of Canada, and a charter member of the Canadian Society of Technical Agriculturists.

Dr. Swaine laid the foundations of forest entomology in Canada during his term of office as Associate Dominion Entomologist. His work on the control of the European spruce sawfly, a pest that, for a time, threatened the entire spruce forests of North America, was one of his greatest contributions.

In 1934 he left the field of forest entomology and became Director of Research for the Department of Agriculture. He held this position until the department's reorganization and his appointment in 1937 to the Directorate of Science Service.

Dr. Swaine's activities were not confined to his official duties. He made friends easily and took a personal interest in his staff and in the life of the community in which he lived. An ardent fisherman, he loved the forest and the outdoors. At home his hobbies were reading, particularly of ancient and prehistory, and drawing in pastels.

In 1905 he was married to Mary Creelman of Truro, Nova Scotia, who celebrated with him their golden wedding anniversary on March twenty-eighth, 1955. Their daughter, Allison, married Dr. I. Timonin, formerly with the Division of Bacteriology in the Department of Agriculture at Ottawa. Dr. and Mrs. Timonin, who have four children, are now residents in Mobile, Alabama. The oldest grandson, Ivan, is a student at Carleton College, Ottawa, and lives with Mrs. Swaine at the family home, 484 Brierwood Avenue.

THE RUNGE PRESS LIMITED, OTTAWA
Mailed: Monday, November 21, 1955